

Quantifying the balance between bycatch and predator or competitor release for nontarget species

EMILIUS A. AALTO¹ AND MARISSA L. BASKETT

Department of Environmental Science and Policy, 1 Shields Avenue, University of California, Davis, California 95616 USA

Abstract. If a species is bycatch in a fishery targeted at its competitor or predator, it experiences both direct anthropogenic mortality and indirect positive effects through species interactions. If the species involved interact strongly, the release from competition or predation can counteract or exceed the negative effects of bycatch. We used a set of two- and three-species community modules to analyze the relative importance of species interactions when modeling the overall effect of harvest with bycatch on a nontarget species. To measure the trade-off between direct mortality and indirect positive effects, we developed a “bycatch transition point” metric to determine, for different scenarios, what levels of bycatch shift overall harvest impact from positive to negative. Under strong direct competition with a targeted competitor, release from competition due to harvest leads to a net increase in abundance even under moderate levels of bycatch. For a three-species model with a shared obligate predator, the release from apparent competition exceeds direct competitive release and outweighs the decrease from bycatch mortality under a wide range of parameters. Therefore, in communities where a shared predator forms a strong link between the target and nontarget species, the effects of indirect interactions on populations can be larger than those of direct interactions. The bycatch transition point metric can be used for tightly linked species to evaluate the relative strengths of positive indirect effects and negative anthropogenic impacts such as bycatch, habitat degradation, and introduction of invasive species.

Key words: *apparent competition; bycatch; competitive release; fisheries management; indirect effects; multispecies fisheries models; predation release.*

INTRODUCTION

While anthropogenic activities (e.g., habitat loss, pollution, climate change, harvest) directly affect the vital rates of many organisms, they also have indirect effects through impacts on competitors, predators, and mutualists. Indirect effects are common in human-dominated ecosystems and pose a challenge to predictability for conservation and management (Wootton 1994, Dickman 2008). These effects are frequently negative, such as increased nest predation due to habitat fragmentation (Harrison and Bruna 1999) or increased competition and predation from introduced species (Clavero and García-Berthou 2005). Indirect effects can also be positive, however, through release from predation or competition. For example, habitat destruction can benefit lesser competitors (Nee and May 1992, McCarthy et al. 1997) or diminish the abundance of predators more than prey (Bascompte and Solé 1998, Swihart et al. 2001). A key question, then, for management that accounts for multiple species and their interactions is how these direct and indirect effects interact to drive overall change in abundance (Mills et

al. 1993, Simberloff 1998, Crowder et al. 2008, Pine et al. 2012).

Over the last few decades, there has been a shift toward ecosystem-based fisheries management in many fisheries due to the limitations of single-species management (May et al. 1979, Ströbele and Wacker 1991, Larkin 1996, Zabel et al. 2003, Pikitch et al. 2004). Direct impact on harvested species has historically been quite high (Jackson et al. 2001, Myers and Worm 2003), and species that are not intended targets of the fishery can also experience direct negative impacts through bycatch mortality. For the rockfish species assemblage in the Bering Sea (*Sebastes*), for example, bycatch mortality from other fisheries is equal to the total harvest from the rockfish fishery itself (Alverson et al. 1994). Bycatch exceeds 50% of total harvested biomass in some fisheries, particularly shrimp trawling, and mortality rates are typically high even if nontarget individuals are released (Alverson et al. 1994, Hall 1996, Hall et al. 2000). Affected species can be found in every trophic level, and bycatch can cause rapid decline across families (Lewison et al. 2004). Despite the many approaches that have been employed to reduce bycatch rates, bycatch mortality for some threatened species is still high enough that bycatch quotas are used to manage the fishery, rather than harvest quotas of the target species (for example, in the Alaska groundfish fishery [Hall et al. 2000]).

Manuscript received 28 July 2012; accepted 21 November 2012; final version received 11 January 2013. Corresponding Editor: K. Stokesbury.

¹ E-mail: aalto@ucdavis.edu

In addition to direct effects on nontarget species, positive indirect effects on nontarget species are particularly common in marine systems due to heavy harvest pressure on specific species (Pimm and Hyman 1987) and include both predation release (e.g., Frank et al. 2005, Frid et al. 2008, Madin et al. 2010) and competitive release (e.g., Fogarty and Murawski 1998, Dulvy et al. 2000, Jenkins 2004, Okey et al. 2007). Such indirect effects can have broad ecosystem impacts (Goñi 1998, Jennings and Kaiser 1998) and can fundamentally restructure communities (Frank et al. 2005, Heithaus et al. 2008). For example, recovery of New England cod fisheries may be hindered by depensation effects on recruitment (i.e., prey competition suppresses with juvenile predators) after shifting to a prey-dominated community (Walters and Kitchell 2001). Release from competition and predation due to heavy harvest and bycatch of cod and Pacific Ocean perch in the Gulf of Alaska in the 1960s may have caused a community-wide shift in abundances, with walleye pollock and arrowtooth flounder greatly outnumbering all other species in a later survey (Alverson et al. 1994).

Accounting for the effects of bycatch is a major part of fisheries management decisions, both for commercial and conservation purposes (Alverson et al. 1994, Hall 1996, Hall et al. 2000, Plagányi et al. 2007). Bycatch is inherently a multispecies concept, and the overall effect of harvest depends on both direct mortality and indirect effects through species interactions. Previous multispecies fisheries models (reviewed in Hollowed et al. 2000, Baskett 2007) tend to fall into two categories: simplified two-species models without indirect interactions (e.g., Ströbele and Wacker 1991, Yodzis 1994, Spencer and Collie 1995, Ströbele and Wacker 1995, Essington 2004) or highly complex food-web models with many interacting species (e.g., Hinke et al. 2004, Walters et al. 2005). Most models do not incorporate the effects of bycatch in a multispecies context (exceptions include Plagányi et al. 2007, Harvey et al. 2008, Kellner et al. 2010). The overall effect of harvest on nontarget species is dependent on the relative strengths of both negative and positive effects. While bycatch mortality generally decreases abundance of nontarget species, harvest can still lead to increases in the nontarget species if the indirect positive effects are sufficiently strong.

To explore the relative importance of indirect effects on community dynamics and determine which types of interactions are most likely to counteract direct negative effects, we develop a set of two- and three-species models of competition and predation. For simplicity, we use the community module approach that can represent strongly interacting sets of species or guilds (Holt 1996, Brose et al. 2005). The modules we explore are direct competition, predation, and apparent competition, a combination of the first two. Apparent competition is an important but often overlooked indirect interaction (Holt 1977, Abrams 1998) in which one species is negatively affected by a competing species through the

increased abundance of a shared predator. It is prevalent in natural systems (Chaneton and Bonsall 2000, Bascompte and Melián 2005) and is often strengthened by human activities such as the introduction of exotic species (Noonburg and Byers 2005, DeCesare et al. 2010). By extending two-species models to include apparent competition, we explore how indirect species interactions alter predicted two-species outcomes while still maintaining simplified community module dynamics.

For the direct-competition and predator-prey models, we assess which factors (e.g., growth rate, relative bycatch susceptibility, strength of species interaction) most affect post-harvest equilibrium abundance of the nontarget species and under what conditions competitive or predation release counteract bycatch mortality. We then use a predator-prey-prey model to analyze the effect of apparent competition on nontarget equilibrium abundance and compare the contributions of competitive and predation release in the three-species context. A better understanding of the relative strengths of indirect positive effects and direct anthropogenic mortality will help clarify which types of species interactions are most important to ecosystem-based management.

METHODS

Model overview

We explore three models: a two-species direct-competition model (DC), a two-species predator-prey model (PP), and a three-species apparent-competition model (AC). The direct-competition model represents competition between a harvested target species (abundance T_t at time t) and a nontarget species (N_t ; Fig. 1a). The two-species predator-prey model represents a targeted obligate predator (abundance P_t) and a nontarget prey species (N_t ; Fig. 1b). The apparent-competition model combines the previous two models into a three-species interaction with two prey species and one shared predator, where the target species (abundance T_t) and nontarget species (N_t) can compete directly while sharing an obligate unfished predator (P_t ; Fig. 1c). We include the potential for direct competition here to determine its effect relative to the apparent competition that arises from these dynamics. In all three models, the nontarget species experiences bycatch, and we quantify under what conditions competitive and/or predation release outweighs bycatch and what maximum bycatch levels would be necessary to avoid a decrease in the abundance of the nontarget species.

Direct-competition model (DC)

For all three scenarios, we use discrete-time models with no generational overlap and model prey growth and competition with modified Beverton-Holt density dependence; see Appendix A for Ricker formulation and results. Abundance for the target species in the next time step (T_{t+1}) depends on its growth factor R and its

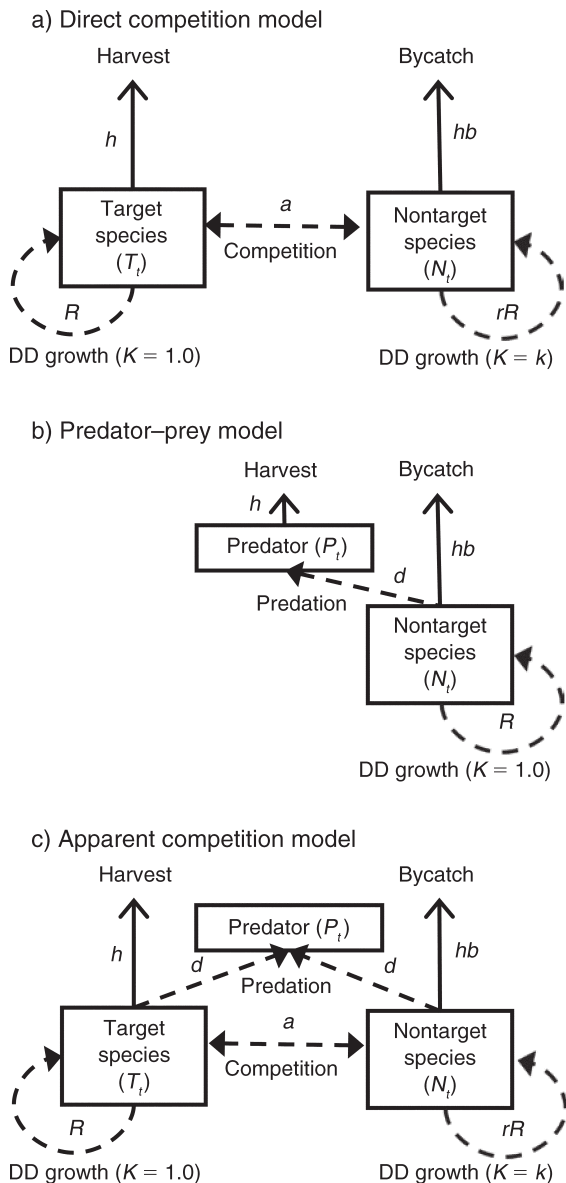


FIG. 1. Model structures. Solid lines indicate anthropogenic effects, and dashed lines indicate intra- or interspecific effects. Parameters and variables are defined in Table 1. (a) Direct-competition model. The target species (abundance T_t) and nontarget species (N_t) exhibit density-dependent (DD) Beverton-Holt growth and competition. Harvest is proportional for the target and nontarget species, modified by the relative bycatch susceptibility of the nontarget species. (b) Predator-prey model. This model is similar to the prior model, except there is no target prey species and the predator (abundance P_t) is harvested. (c) Apparent-competition model. The parameters in this model are a combination of the prior two models. One prey species (abundance T_t) is targeted by harvest while the other (N_t) experiences bycatch, and the predator (P_t) is not directly affected by harvest. Both prey species are consumed by the predator.

current abundance T_t , the current abundance of its competitor (N_t) and the competitive effect a of N_t individuals relative to an individual of T_t . Population size is scaled to set carrying capacity (K) to one, making T_t a proportional abundance (specifically, proportional to equilibrium biomass in the absence of species interactions and harvest; see Appendix B for non-dimensionalization). A constant proportion h of T_t is harvested each time step. We use a constant harvest proportion for analytical tractability, a harvest model commonly used in the literature (e.g., Yodzis 1994, Gardmark et al. 2003, Potts and Vincent 2008); see Appendix C for constant escapement harvest formulation and results.

The nontarget prey species (abundance N_t) changes in a similar manner to the target species. Its growth factor and carrying capacity are scaled relative to those of the target species using the parameters r and k , respectively. We assume strength of competition to be symmetric. Note that N_t is measured relative to the carrying capacity of the target species, not its own carrying capacity (if different), in order to have a uniform scaling for all species. Bycatch mortality in the nontarget species occurs proportionally to the harvest of the target species, scaled by the relative bycatch susceptibility parameter b that represents the proportion of harvest h experienced by the nontarget species. Note that $b > 1$ is possible if the nontarget species experiences higher mortality than the target species. Therefore, the direct-competition model (Fig. 1a) is

$$T_{t+1} = \frac{RT_t}{(1 + (R - 1)(aN_t + T_t))} (1 - h) \quad (1)$$

$$N_{t+1} = \frac{rRkN_t}{(k + (rR - 1)(N_t + aT_t))} (1 - hb). \quad (2)$$

We focus on the effects of relative bycatch susceptibility b and competition strength a , with $r = k = 1$ (Table 1). A more realistic assumption is that the two species will not be demographically identical. Many bycaught species, such as some rockfish, are of conservation interest precisely because of their low populations and slow growth rates (e.g., Harvey et al. 2008). Therefore, we also analyze the effects of changes to relative growth factor r and relative carrying capacity k . We set growth factor R to a moderate value for the target species to allow a reasonably high harvest proportion and the possibility of broad variation in the nontarget species growth factor. We presume that intraspecific competition is greater than interspecific competition and set the default strength of competition a to one half. This allows a stable coexistence equilibrium and ensures that the density dependent effects of harvesting a competitor are lower than those from direct mortality. We do not intend these values to reflect the characteristics of a specific community, but to serve as biologically relevant

TABLE 1. Model symbol definitions and values.

Symbol	Definition	Default	Range	Models
State variables				
T_t	abundance of target prey species at time t			DC, AC
N_t	abundance of nontarget species at time t			DC, PP, AC
P_t	abundance of predator at time t			PP, AC
$\bar{T}, \bar{N}, \bar{P}$	equilibrium abundance of each species			DC, PP, AC
Parameters				
R	Beverton-Holt growth factor for target species	1.5	1.05–2.0	DC, PP, AC
K	carrying capacity of target species	1.0		DC, PP, AC
r	nontarget growth factor relative to target species	1.0	0.75–1.5	DC, AC
k	nontarget carrying capacity relative to target species†	1.0	0.5–1.5	DC, AC
a	strength of competition between the two prey species	0.5	0.0–0.95	DC, AC
d	predation capture scaled by conversion	1.25	1.0–2.0	PP, AC
h	proportion of target species harvested per time step	0.1/0.02‡	0.0–0.3	DC, PP, AC
b	nontarget bycatch susceptibility relative to target species	0.5	0.0–1.0	DC, PP, AC
Analysis				
\hat{b}	bycatch transition point§			DC, PP, AC

Notes: All values are unitless. See Appendix B for non-dimensionalization. Models are: DC, direct competition; PP, predator-prey; AC, apparent competition.

† Target species carrying capacity is scaled to 1.0 in the DC and AC models.

‡ Default value for DC and AC models is $h = 0.1$, and $h = 0.02$ for the PP model.

§ See *Methods: Analysis* for explanation.

defaults while exploring the sensitivity of the model over a range of values.

Predator-prey model (PP)

Predation in the two-species predator-prey model (Fig. 1b) follows Nicholson-Bailey dynamics (Nicholson and Bailey 1935). Dynamics for the prey species are similar to those described above in the DC model (Beverton-Holt growth with growth factor R) with a new term for predation. The predator with abundance P_t is a specialist on the prey species (N_t). The predation parameter d incorporates both capture and conversion such that predation probability is exponentially proportional to dP_t . P_t is measured in units of “effective proportional abundance,” or proportion of the prey species’ carrying capacity multiplied by the original conversion rate (see Appendix B). The predator is the target of harvest, with bycatch affecting the prey species. The predator-prey model is

$$N_{t+1} = \frac{RN_t}{(1 + (R - 1)N_t)} e^{-dP_t}(1 - hb) \quad (3)$$

$$P_{t+1} = N_t(1 - e^{-dP_t})(1 - h). \quad (4)$$

We set the predation parameter d to a low enough level to allow coexistence in both the two- and three-species models across most of the parameter ranges. The low predator growth rate necessitated a lower default value of h for the PP model (Table 1).

Apparent-competition model (AC)

The three-species model has two competing prey species (target species T_t and nontarget species N_t) and one shared obligate predator (P_t ; Fig. 1c). It combines the dynamics of the two models described above, with

Beverton-Holt growth (growth factors R and rR) and competition (relative competition effect a), Nicholson-Bailey predation, and constant-proportion harvest (h) on one of the two prey species. As a simplification, we assume the predator treats individuals of both prey species equally, with the same predation parameter d for both. We additionally assume that bycatch affects only the nontarget prey species and not the predator. The apparent-competition model is

$$T_{t+1} = \frac{RT_t}{(1 + (R - 1)(aN_t + T_t))} e^{-dP_t}(1 - h) \quad (5)$$

$$N_{t+1} = \frac{rRkN_t}{(k + (rR - 1)(N_t + aT_t))} e^{-dP_t}(1 - hb) \quad (6)$$

$$P_{t+1} = (N_t + T_t)(1 - e^{-dP_t}). \quad (7)$$

We analyze the relative effect of direct competitive release (dependent on parameter a) vs. apparent competitive release (dependent on parameter d) and compare results to the two-species interactions in the direct-competition and predator-prey models. Because the predator is not directly harvested in the AC model, we compare the results of direct predation release via harvest and indirect predation release through apparent competition.

Analysis

Our primary goal is to examine how bycatch interacts with indirect effects to determine whether harvest has an overall positive or negative effect on the final abundance of nontarget prey species. Our central metric is the “bycatch transition point” \hat{b} , which is the bycatch level at which the overall harvest effect on the equilibrium abundance \bar{N} of the nontarget species transitions from

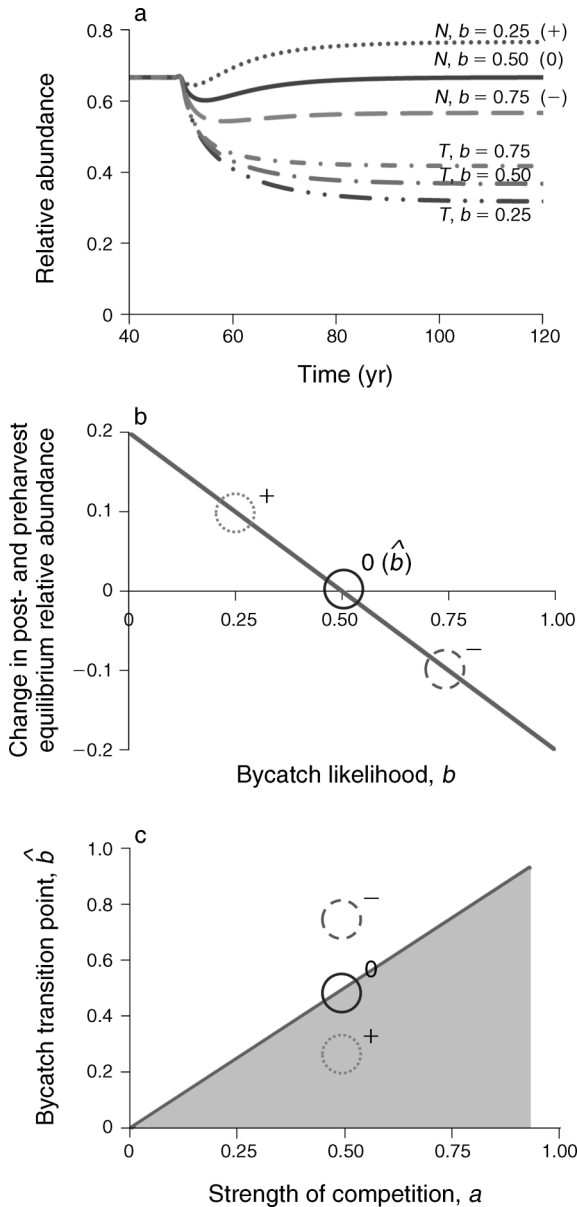


FIG. 2. Sample time series and bycatch transition for the direct-competition model. (a) Time series for low, medium, and high bycatch susceptibility ($b = 0.25, 0.50,$ and 0.75 respectively) showing change in abundance N_t and T_t for nontarget species and target species, respectively, with fishing started at $t = 50$. With the default values for the DC model, equilibrium nontarget abundance \bar{N} decreases (-) if $b > 0.5$ and increases (+) if $b < 0.5$. (b) Change in \bar{N} post-harvest vs. relative bycatch susceptibility b . The three equilibria from panel (a) are indicated, as is the bycatch transition point \hat{b} . (c) Bycatch transition point \hat{b} vs. strength of competition a . The equilibria from panel (a) are indicated for default competition parameter $a = 0.5$. If relative bycatch susceptibility falls within the shaded region under the line for a given value of a , harvest will have an overall positive effect. Above the line, the effect will be negative. This is equivalent to the reduced form of Eq. 10 which, for the default values of r and k , simplifies to $\hat{b} = a$.

positive to negative (Fig. 2). Indirect positive interaction effects are stronger than direct bycatch mortality if relative bycatch susceptibility is below this level and weaker if above it. We explore sensitivity of this metric to all parameter values to determine which parameters have the greatest effect on the population response to bycatch and which indirect interactions most strongly affect overall harvest effect.

We can analytically derive the formula for the bycatch transition point in the DC model, and we numerically determine it in the PP and AC models. To find \hat{b} analytically, we first solve for the equilibrium abundance $\bar{N} = N_t = N_{t+1}$ of the nontarget species:

$$\bar{N} = \left(k \frac{rR(1-hb) - 1}{rR - 1} - a \frac{R(1-h) - 1}{R - 1} \right) / (1 - a^2). \quad (8)$$

The target species, not shown here, is also at equilibrium $\bar{T} = T_t = T_{t+1}$. At the bycatch transition point, direct bycatch mortality and indirect positive effects are in balance and the overall effect of harvest on the nontarget species is neutral. Consequently, changing harvest levels has no effect on \bar{N} if $b = \hat{b}$. We find the change in \bar{N} with respect to harvest by first taking the partial derivative $\partial \bar{N} / \partial h$:

$$\frac{\partial \bar{N}}{\partial h} = \left(\frac{a}{R - 1} - \frac{krb}{rR - 1} \right) \left(\frac{R}{1 - a^2} \right). \quad (9)$$

Then the bycatch transition point is found by setting $\partial \bar{N} / \partial h = 0$ and solving for b :

$$\hat{b} = \frac{a(rR - 1)}{rk(R - 1)} \quad \text{when} \quad \frac{\partial \bar{N}}{\partial h} = 0. \quad (10)$$

To solve for \hat{b} numerically, we compare equilibrium abundance before harvest ($\bar{N}_{h=0}$) and after harvest ($\bar{N}_{h>0}$) over a range of relative bycatch susceptibility values. We first run each model without harvest until equilibrium abundances are reached ($N_{t+1} - N_t < 0.0001$), then implement harvest and continue running until a new equilibrium is reached. The value of b for which both indirect positive and direct negative effects of harvest have balanced out and there is no change in equilibrium ($\bar{N}_{h>0} = \bar{N}_{h=0}$) is the transition point (Fig. 2). For the DC model, this formulation leads to mathematically equivalent results as eq. 10. For the PP and AC models, equilibrium points were reached within 50 time-steps for almost all instances. Consequently, we did not evaluate transient dynamics. Note that the bycatch transition graph only shows the point at which overall harvest effect on the equilibrium abundance of the nontarget species \bar{N} shifts from positive to negative. It does not show final abundance or magnitude of the harvest effect, both of which depend on all parameter values. We calculate \hat{b} across the range of values for each parameter given in Table 1, while setting all other parameters to their default values. All analysis was done using R 2.14.1 (R Development Core Team 2012).

RESULTS

Direct-competition model (DC)

The net effect of harvest on the nontarget species in the direct-competition model depends primarily on both the strength of competition a and the relative bycatch susceptibility b , with competitive release stronger than bycatch mortality if $a > b$ (Fig. 3a; the direct-competition model is indicated by the solid line in the following figures). Growth factor R does not affect the bycatch transition point \hat{b} if $r = 1$ (the default value; Fig. 3b), because it is the relative rather than absolute growth rates of the target and nontarget species that determine the ability of the nontarget species to increase following competitive release. As relative growth factor r decreases, \hat{b} drops rapidly (Fig. 3c). In contrast, \hat{b} decreases with increasing k , the relative carrying capacity of the nontarget species (Fig. 3d). This result occurs because a lower carrying capacity for the nontarget than the target species leads to a higher relative abundance of the target species and therefore greater competitive pressure on the nontarget species. As expected from Equation 10, harvest proportion h has no effect on \hat{b} (Fig. 3e). This is similar to the comparison between the growth factors r and R : relative mortality, rather than absolute, determines nontarget response.

The bycatch transition point for the Ricker model was nearly identical for all parameters except for low values for r and high h (Appendix A). Nontarget species following Ricker growth are less sensitive to bycatch than predicted if assuming Beverton-Holt growth. Results from constant escapement harvest were virtually identical to constant-proportion harvest (Appendix C).

Predator-prey model (PP)

Harvest of a predator had a much stronger indirect positive impact on the nontarget prey than harvest of a competitor, and the transition from positive to negative effects of harvest on the nontarget species took place at higher values of relative bycatch susceptibility. The bycatch transition point \hat{b} was almost always much higher than for the other two models and this varied only slightly with prey growth rate R , harvest level h , and strength of predation d (dotted line in Figs. 3b, e, f). There is a narrow range at low values within which \hat{b} is sensitive to the value of d (Fig. 3f). Below that range, the predator cannot persist and above it the strength of predation no longer affects the bycatch transition point, though it does affect equilibrium abundance (not shown). Note that the predator is more sensitive to harvest than the target prey species and can only persist at low harvest levels.

Apparent-competition model (AC)

The apparent-competition model includes both species interactions from the DC and PP models, with one predator and two competing prey species. Unlike with the DC model, however, harvest produced a net increase

in equilibrium nontarget prey abundance \bar{N} even if the relative bycatch susceptibility was greater than the strength of competition. The nontarget species in the three-species system is less sensitive to bycatch for all parameters (dashed lines in Figs. 3a–e), indicating that release from apparent competition increases \bar{N} under higher bycatch levels than simple direct competitive release.

The increased positive effect of harvest on \bar{N} is due to the combination of two positive indirect effects, reduced pressure from both direct and apparent competition. The value of \hat{b} is greater across all parameters under apparent competition in the three-species system than under direct competition alone. Note that even if there is no direct competition ($a = 0$ in Fig. 3a) the level of bycatch necessary to cause an overall decrease in abundance is still high relative to almost all parameter values for the direct-competition model. Although the model parameters do affect the specific value of the bycatch transition point, that variation is limited to a narrow range of relative bycatch susceptibility. The strength of predation does not strongly affect this range, provided that the three-species system is stable (dashed line in Fig. 3f). For some parameter ranges (low R , high h , low d) the predator can no longer persist and the system reverts to a two-species direct-competition equilibrium.

DISCUSSION

The results from our two- and three-species models suggest that indirect positive effects from harvest can be as strong as or stronger than direct negative impact when the nontarget species is tightly linked to the target species via negative interactions. Even without a direct interspecific interaction, a positive effect through a third species can still counter direct negative effects on the nontarget species. The strongest positive effects occur when a strongly interacting obligate predator is present in the system, regardless of whether or not the predator is directly harvested (dashed and dotted lines, Fig. 3). Furthermore, release from apparent competition had a large positive indirect effect even in the absence of direct competition (dashed line, $a = 0$, Fig. 3a). This effect was stronger than all but the highest levels of direct competitive release when considered alone, though high interspecific competition also increases the potential for a positive effect from harvest.

Our results also indicate which characteristics would make a particular species less likely to decrease in abundance despite direct anthropogenic mortality, provided that a competitor or predator is also experiencing high mortality. A lessened negative or overall positive response by the nontarget species is more likely with stronger competition (Fig. 3a), greater relative growth rate (Fig. 3c), and lower relative carrying capacity (Fig. 3d). Finally, the most important factor in these models was the presence of a strong predator. Even the small decrease in predator abundance follow-

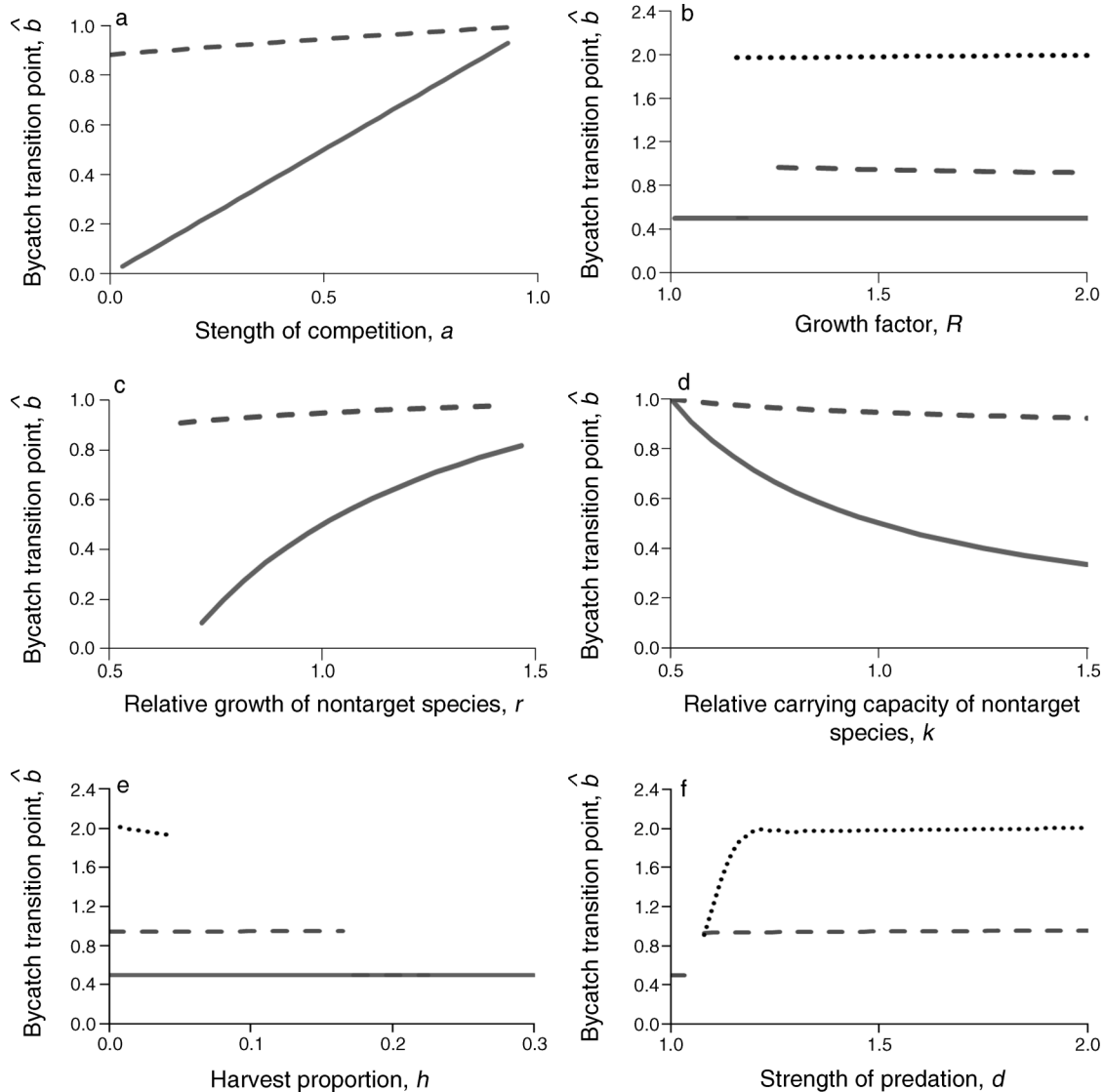


FIG. 3. Bycatch transition point \hat{b} for all models and parameters. The bycatch transition point is the value of relative bycatch susceptibility at which overall harvest effect on nontarget species transitions from positive to negative. Solid lines indicate direct-competition (DC) model results, dotted lines indicate predator-prey (PP) model results, and dashed lines indicate apparent-competition (AC) model results. The lines end if a full multispecies equilibrium was not possible beyond that value, or are omitted if the parameter is inappropriate to that specific model. (a) Strength of competition a between the target species and nontarget species. (b) Absolute growth factor of the prey species. (c) Relative growth factor r of the nontarget vs. target species. (d) Relative carrying capacity k of the nontarget vs. target species. (e) Harvest proportion h of the target species (or predator in PP model). (f) Strength of predation d . Note differences in y -axis scales in panels (a), (c), and (d) vs. (b), (e), and (f).

ing harvest of one prey species in the AC model was enough to outweigh high levels of bycatch for the nontarget prey species. This effect would be magnified if the predator experienced bycatch as well, which can be expected in many marine fisheries given that multiple trophic levels are often targeted (Lewison et al. 2004).

Species interactions are most likely to produce strong indirect effects when abundances are low, a common state for species in fisheries or targeted for conservation (Walters and Kitchell 2001). Predation release is

expected to be stronger than direct competitive release in systems where predation, not solely harvest, contributes to keeping both species well below their normal carrying capacities (Holt et al. 1994), and the potential for strong positive indirect effects is further magnified if the predator is shared (Holt 1977, Abrams 1998). A single-species model for the nontarget species in our example fishery that considers only bycatch would miss the strong positive effect of reduced apparent competition and consequently would overestimate the negative

effects of harvest as a whole. This overestimation might lead to expensive bycatch mitigation efforts such as a shortened fishing season when such measures were unnecessary.

Example systems and management implications

There is ample evidence in aquatic systems of the potential for positive indirect effects to outweigh direct negative impact. For example, multiple species have increased in abundance after harvest despite moderate bycatch mortality. In the review by Christensen (1996), several systems, primarily lakes, exhibited an increased prey abundance following increased harvest of predators despite harvest of the prey as well. Competitive release due to overfishing of native trout in the Great Lakes allowed non-native lamprey and alewife to rapidly increase in number (Pimm and Hyman 1987). Both small skates (Dulvy et al. 2000) and urchins (Jenkins 2004) have increased in abundance after local fisheries intensively targeted competitors (larger skate species and abalone, respectively). Frid and Marliave (2010) found that both trophic cascades and apparent competition mediated by lingcod and rockfish have diminished due to high harvest in a temperate reef system. More generally, heavy bycatch impact often includes predators that are not directly targeted, such as marine mammals and some shark species, and a decline in top marine predators has restructured many communities (Heithaus et al. 2008). In such cases, the predator often receives a dual negative effect through both direct bycatch mortality and loss of prey. We have focused on positive indirect interactions because only the balancing of negative and positive effects leaves the directionality of the outcome uncertain.

Though the single-species approach is still common (Whipple et al. 2000), multispecies models are increasingly used in fisheries and conservation management and frequently predict different management outcomes than single-species models (e.g., May et al. 1979, Finnoff and Tschirhart 2003). For example, analysis using age-structured predator-prey models suggests that overall harvest effect on bycaught rockfish in a hake fishery varies, with predation release outweighing moderate bycatch mortality for the faster-growing species only (Harvey et al. 2008). Similarly, competitive release between sardines and anchovies in South Africa was not strong enough to counteract high inter-fishery bycatch levels, necessitating a single management strategy to maintain both fisheries sustainably (Plagányi et al. 2007).

A particularly informative example of bycatch-structured management is the Gulf of Alaska groundfish fishery, in which the allowable fishing effort for target species is determined by bycatch quotas of “prohibited species” such as halibut (Witherell and Pautzke 1997). Species abundances have shifted dramatically over the past decades but the most likely candidate in the fishery for strong positive indirect effects from harvest appears

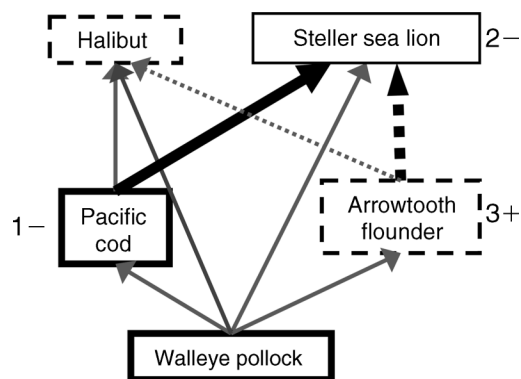


FIG. 4. Gulf of Alaska Pacific cod and walleye pollock fishery wherein the arrowtooth flounder illustrate potential release from apparent competition. The cod and pollock fisheries (heavy outlines) cause moderate bycatch on both halibut and flounder (dashed outlines; Alverson et al. 1994). Flounder, halibut, cod, and Steller sea lions are the four most important pollock predators, and both halibut and sea lions consume cod and flounder as well (Dorn et al. 2011). Arrowtooth flounder, though the dominant predator of pollock, consumes a diversity of prey and competes with its own predators (dotted lines). Heavy lines indicate a possible apparent-competition pathway through which (1) decrease in cod has contributed to (2) sea lion decline and (3) increase in flounder due to lowered predation.

to be the arrowtooth flounder, which has increased in both relative and absolute abundance despite moderate bycatch (Alverson et al. 1994, Goñi 1998, NPFMC 2011). Recent decreases in cod abundance (Alverson et al. 1994, NPFMC 2011) due to the cod fishery may have contributed to the decades-long decline in Steller sea lion populations (Merrick et al. 1987, Thompson et al. 2011), potentially releasing arrowtooth flounder from apparent competition (bold lines; Fig. 4). Though this scenario suggests similar dynamics to our AC model, there are many potential complicating factors. Sea lion abundance is also tightly linked to pollock, a species whose abundance is driven by bottom-up forces (Dorn et al. 2011). Flounder shares many prey species with its own predators and an increase in flounder abundance may further decrease cod, halibut, and sea lion abundances through increased intra-guild competition (Dorn et al. 2011, Turnock and Wilderbuer 2011). Sea lions may be experiencing nutritional stress due to long-term diet shifts, rather than responding to lowered prey abundance (Trites and Donnelly 2003). Though previous Alaskan fishery models have typically limited predation effects to at most an augmented single-species approach without multispecies dynamics (e.g., Jurado-Molina et al. 2005), Van Kirk et al. (2010) confirmed the importance of complex interactions by finding that including dynamic predation and competition over prey in a pollock-cod-flounder model produced a better fit for observed age distributions and mortality patterns than the single-species alternative. Our results further indicate which species interactions—in particular, apparent competition—will likely be crucial when con-

structing more complex, tactical models applied to this and other relevant systems.

One limitation to the application of our model is that species interactions parameters, especially for abstracted models such as the ones presented here (e.g., competition strength a and predation strength d), are difficult to measure in practice (Whipple et al. 2000) although statistical advances in data analysis are making their estimation more feasible (Minto and Worm 2012). Parameter estimation is less of a concern when apparent competition is the central dynamic, as the AC model is relatively insensitive to parameter value. Empirical work is not only necessary to parameterize models, but our models and results suggest the need for empirical investigation to validate model assumptions concerning the symmetric strength of competition and predator functional form (i.e., Nicholson-Bailey vs. Lotka-Volterra).

Model assumptions

As with any model, our model necessarily has a number of simplifying assumptions; in particular, the focus on a specific set of strong interacting species. In our AC model, the net increase of the bycaught species relied primarily on a decrease in a predator shared with the targeted species. Firstly, the nontarget species may experience no decrease in predation if the predator can increase its effectiveness by focusing on only one species (Spencer and Collie 1995, Chase et al. 2002). More importantly, marine predators are often generalists, with a large array of prey such that a decrease in one species will not strongly affect the predator's abundance (e.g., Paine 1992, Bascompte et al. 2005). Models with generalist predators show that predation release would be much lower if the predator's dynamics were less determined by the abundance of the two prey species (Abrams and Matsuda 1996, Swihart et al. 2001). However, although an immediate numerical response by the predator may be unrealistic, similar dynamics can occur with mobile, non-territorial predators via short-term aggregation in response to prey increase (Holt and Kotler 1987), a common feature of marine systems (e.g., Veit et al. 1993, Anderson 2001). These assumptions are less critical to the bycatch response of the PP model because direct predator harvest, whether generalist or obligate, would release the nontarget prey from predation. Similarly, although we did not model predator bycatch in the AC model we would expect further predator reduction to increase the positive effects of harvest on the nontarget species. Direct predator mortality will release the target species as well and may dampen some of the positive nontarget effect at higher competition levels. Our model predator was particularly sensitive to direct harvest, however, and a real-world predator with multiple prey and a robust age-structured population might tolerate greater harvest pressure before collapsing. Although not analyzed here, we would expect harvest of an intra-guild predator to

also show a strong blend of predation and competitive release, particularly if the intra-guild prey is a superior competitor (Holt and Polis 1997).

Similarly, the strength of competitive release in the DC and AC models depends on our use of ecologically similar competitors in a tightly linked system. Marine systems are often open, with complex food webs and many weak interactions that may diffuse indirect effects through multiple competing species (Polis and Strong 1996). Additionally, many bycaught species of conservation management concern are trophically distant from the target species (e.g., sea turtles, marine mammals [Lewison et al. 2004]) or have much lower growth rates (e.g., hake and canary rockfish [Harvey et al. 2008]). Species with little direct ecological relationship would not be expected to experience the strong indirect positive effects seen in our simulation. Even if the target and nontarget species are more directly linked, if the nontarget species reproduces much more slowly (i.e., low r value) we would not expect to see a positive response unless bycatch is extremely low or predation release is high (Fig. 3c). In general, the model results may not be applicable if the two species have very different life histories, such as not breeding with the same regularity.

Generally speaking, community structure and strength of species interactions are critical to an accurate model (Yodzis 1994, Hollowed et al. 2000, Essington 2004) but can be very difficult to quantify, particularly for an open system (Abrams and Ginzburg 2000, Hill et al. 2007). As system complexity increases, accurate prediction becomes less likely (Noy-Meir 1981, Walters et al. 2005), though not all weak interactions are important to overall dynamics (Yodzis 1998). Due to the difficulties involved with accurately modeling an entire food web, the community module approach used here remains a valuable tool (Whipple et al. 2000, Bascompte and Melián 2005) and applies particularly well to fisheries, which disproportionately involve strong interactors by targeting upper trophic levels (Bascompte et al. 2005).

We did not consider additional harvest methods beyond constant proportion and constant escapement (Appendix C), and assumed that breeding and harvest events occurred once per year. Bycatch effects may differ if seasonal or pulse harvesting occurs irregularly with regard to breeding, and adding a time-dependent or dynamic-effort harvest term would allow exploration of more complex harvest methods. Another possible future direction is the incorporation of age structure throughout the model, which would allow us to model size-specific harvest strategies. One potential topic for a size-structured model is how same-species bycatch of smaller nontarget individuals (e.g., below a minimum size limit) might affect population dynamics, particularly in situations with strong adult-juvenile competition or cannibalism.

Beyond bycatch

While our example model focuses on fisheries and bycatch, similar effects could be found in other systems where anthropogenic activities affect multiple interacting species to different degrees. If the nontarget species is invasive or otherwise undesirable, then minimizing indirect positive effects would be one component of managing its spread. For example, invasive species can benefit from apparent competition against native species (e.g., Norbury 2001, Lau and Strauss 2005, Noonburg and Byers 2005, Orrock et al. 2008) and reducing invasive abundance would have a strong indirect positive effect on the native. As another example, habitat degradation could play an analogous role to harvest and bycatch in a terrestrial system by differentially affecting two competing species. Predicting their corresponding changes in abundance would require an estimate of their level of competition, as well as any shared predators or prey that might create an indirect interaction pathway (Gotelli and Ellison 2006). Theoretical studies have shown that one species can become more numerous despite losing habitat overall, an outcome particularly likely if competition is asymmetrical (Nee and May 1992, McCarthy et al. 1997) or a strong predator is present (Bascompte and Solé 1998, Swihart et al. 2001, Melián and Bascompte 2002). Though functionally different and focused on habitat occupancy rather than abundance, these models find results similar to ours: below a specific threshold, direct negative impact (habitat degradation) can have a neutral or overall positive effect on one species if the negative impact on a strong competitor or predator is even greater. The metric we develop here to quantify the balance between these effects, the bycatch transition point, can readily be adapted to other such scenarios to inform monitoring expectations and management decisions in a multispecies context.

ACKNOWLEDGMENTS

We thank Marcel Holyoak, Alan Hastings, and two anonymous reviewers for valuable suggestions and comments on previous versions of the manuscript. Funding for this project was provided by a SeaGrant fellowship from the National Oceanic and Atmospheric Administration.

LITERATURE CITED

- Abrams, P. A. 1998. High competition with low similarity and low competition with high similarity: exploitative and apparent competition in consumer–resource systems. *American Naturalist* 152:114–128.
- Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* 15:337–341.
- Abrams, P. A., and H. Matsuda. 1996. Positive indirect effects between prey species that share predators. *Ecology* 77:610–616.
- Alverson, D. L., M. H. Freeberg, S. A. Murawski, and J. Pope. 1994. A global assessment of fisheries bycatch and discards. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Anderson, T. W. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82:245–257.
- Bascompte, J., and C. J. Melián. 2005. Simple trophic modules for complex food webs. *Ecology* 86:2868–2873.
- Bascompte, J., C. J. Melián, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences USA* 102:5443–5447.
- Bascompte, J., and R. V. Solé. 1998. Effects of habitat destruction in a prey–predator metapopulation model. *Journal of Theoretical Biology* 195:383–393.
- Baskett, M. L. 2007. Simple fisheries and marine reserve models of interacting species: an overview and example with recruitment facilitation. *CalCOFI* 48:71–81.
- Brose, U., E. L. Berlow, and N. D. Martinez. 2005. Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters* 8:1317–1325.
- Chaneton, E. J., and M. B. Bonsall. 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos* 88:380–394.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5:302–315.
- Christensen, V. 1996. Managing fisheries involving predator and prey species. *Reviews in Fish Biology and Fisheries* 6:417–442.
- Clavero, M., and E. García-Berthou. 2005. Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution* 20:110.
- Crowder, L. B., E. L. Hazen, N. Avissar, R. Bjorkland, C. Latanich, and M. B. Ogburn. 2008. The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. *Annual Review of Ecology, Evolution, and Systematics* 39:259–278.
- DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation* 13:353–362.
- Dickman, C. R. 2008. Indirect interactions and conservation in human-modified environments. *Animal Conservation* 11:11–12.
- Dorn, M., K. Aydin, S. Barbeaux, M. Guttormsen, K. Spalinger, and W. Palsson. 2011. Assessment of the walleye pollock stock in the Gulf of Alaska. Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, AK.
- Dulvy, N. K., J. D. Metcalfe, J. Glanville, M. G. Pawson, and J. D. Reynolds. 2000. Fishery stability, local extinctions, and shifts in community structure in skates. *Conservation Biology* 14:283–293.
- Essington, T. 2004. Getting the right answer from the wrong model: evaluating the sensitivity of multispecies fisheries advice to uncertain species interactions. *Bulletin of Marine Science* 74:563–581.
- Finnoff, D., and J. Tschirhart. 2003. Harvesting in an eight-species ecosystem. *Journal of Environmental Economics and Management* 45:589–611.
- Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecological Applications* 8:S6–S22.
- Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621–1623.
- Frid, A., G. G. Baker, and L. M. Dill. 2008. Do shark declines create fear-released systems? *Oikos* 117:191–201.
- Frid, A., and J. Marliave. 2010. Predatory fishes affect trophic cascades and apparent competition in temperate reefs. *Biology Letters* 6:533–536.

- Gardmark, A., U. Dieckmann, and P. Lundbert. 2003. Life-history evolution in harvested populations: the role of natural predation. *Evolutionary Ecology Research* 5:239–257.
- Goñi, R. 1998. Ecosystem effects of marine fisheries: an overview. *Ocean and Coastal Management* 40:37–64.
- Gotelli, N. J., and A. M. Ellison. 2006. Food-web models predict species abundances in response to habitat change. *PLoS Biology* 4:e324.
- Hall, M. A. 1996. On bycatches. *Reviews in Fish Biology and Fisheries* 6:319–352.
- Hall, M. A., D. L. Alverson, and K. I. Metuzals. 2000. Bycatch: problems and solutions. *Marine Pollution Bulletin* 41:204–219.
- Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: What do we know for sure? *Ecography* 22:225–232.
- Harvey, C., K. Gross, V. Simon, and J. Hastie. 2008. Trophic and fishery interactions between Pacific hake and rockfish: effect on rockfish population rebuilding times. *Marine Ecology Progress Series* 365:165–176.
- Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23:202–210.
- Hill, S. L., G. M. Watters, A. E. Punt, M. K. McAllister, C. Le Quere, and J. Turner. 2007. Model uncertainty in the ecosystem approach to fisheries. *Fish and Fisheries* 8:315–336.
- Hinke, J., I. Kaplan, K. AYdin, G. Watters, R. Olson, and J. F. Kitchell. 2004. Visualizing the food-web effects of fishing for tunas in the Pacific Ocean. *Ecology and Society*. 9:10.
- Hollowed, A. B., N. Bax, R. Beamish, J. Collie, M. Fogarty, P. Livingston, J. Pope, and J. C. Rice. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES Journal of Marine Science* 57:707–719.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Holt, R. D. 1996. Community modules. Pages 333–350 in M. Begon and A. Gange, editors. *Multitrophic interactions in terrestrial systems*. Blackwell, London, UK.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* 144:741–771.
- Holt, R. D., and B. P. Kotler. 1987. Short-term apparent competition. *American Naturalist* 130:412–430.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* 149:745–764.
- Jackson, J. B. C., et al. 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science* 293:629–638.
- Jenkins, G. P. 2004. The ecosystem effects of abalone fishing: a review. *Marine and Freshwater Research* 55:545–552.
- Jennings, S., and M. Kaiser. 1998. The effects of fishing on marine ecosystems. Pages 201–302. in J. Blaxter, A. Southward, and P. Tyler, editors. *Advances in marine biology*. Academic Press, Waltham, Massachusetts, USA.
- Jurado-Molina, J., P. A. Livingston, and J. N. Ianelli. 2005. Incorporating predation interactions in a statistical catch-at-age model for a predator–prey system in the eastern Bering Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1865–1873.
- Kellner, J. B., S. Y. Litvin, A. Hastings, F. Micheli, and P. J. Mumby. 2010. Disentangling trophic interactions inside a Caribbean marine reserve. *Ecological Applications* 20:1979–1992.
- Larkin, P. A. 1996. Concepts and issues in marine ecosystem management. *Reviews in Fish Biology and Fisheries* 6:139–164.
- Lau, J. A., and S. Y. Strauss. 2005. Insect herbivores drive important indirect effects of exotic plants on native communities. *Ecology* 86:2990–2997.
- Lewis, R. L., L. B. Crowder, A. J. Read, and S. A. Freeman. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution* 19:598–604.
- Madin, E. M. P., S. D. Gaines, and R. R. Warner. 2010. Field evidence for pervasive indirect effects of fishing on prey foraging behavior. *Ecology* 91:3563–3571.
- May, R. M., J. R. Beddington, C. W. Clark, S. J. Holt, and R. M. Laws. 1979. Management of multispecies fisheries. *Science* 205:267–277.
- McCarthy, M. A., D. B. Lindenmayer, and M. Drechsler. 1997. Extinction debts and risks faced by abundant species. *Conservation Biology* 11:221–226.
- Melián, C. J., and J. Bascompte. 2002. Food web structure and habitat loss. *Ecology Letters* 5:37–46.
- Merrick, R. L., T. R. Loughlin, and D. G. Calkins. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956–86. *Fishery Bulletin* 85:351–365.
- Mills, L. S., M. E. Soule, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219–224.
- Minto, C., and B. Worm. 2012. Interactions between small pelagic fish and young cod across the North Atlantic. *Ecology* 93:2139–2154.
- Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283.
- Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61:37–40.
- Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations. *Proceedings of the Zoological Society of London* 105:551–598.
- Noonburg, E. G., and J. E. Byers. 2005. More harm than good: when invader vulnerability to predators enhances impact on native species. *Ecology* 86:2555–2560.
- Norbury, G. 2001. Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. *Journal of Applied Ecology* 38:1350–1361.
- Noy-Meir, I. 1981. Theoretical dynamics of competitors under predation. *Oecologia* 50:277–284.
- NPFMC. 2011. Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, AK.
- Okey, T. A., B. A. Wright, and M. Y. Brubaker. 2007. Salmon shark connections: North Pacific climate change, indirect fisheries effects, or just variability? *Fish and Fisheries* 8:359–366.
- Orrock, J. L., M. S. Witter, and O. J. Reichman. 2008. Apparent competition with an exotic plant reduces native plant establishment. *Ecology* 89:1168–1174.
- Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355:73–75.
- Pikitch, E. K., et al. 2004. Ecology: ecosystem-based fishery management. *Science* 305:346–347.
- Pimm, S. L., and J. B. Hyman. 1987. Ecological stability in the context of multispecies fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 44:s84–s94.
- Pine, W., III, S. J. Martell, C. Walters, and J. F. Kitchell. 2012. Counterintuitive responses of fish populations to management actions. *Fisheries* 34:165–180.
- Plagányi, É. E., R. A. Rademeyer, D. S. Butterworth, C. L. Cunningham, and S. J. Johnston. 2007. Making management procedures operational—innovations implemented in South Africa. *ICES Journal of Marine Science* 64:626–632.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.

- Potts, M. D., and J. R. Vincent. 2008. Harvest and extinction in multi-species ecosystems. *Ecological Economics* 65:336–347.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Biological Conservation* 83:247–257.
- Spencer, P. D., and J. Collie. 1995. A simple predator–prey model of exploited marine fish populations incorporating alternative prey. *ICES Journal of Marine Science* 53:615–628.
- Ströbele, W. J., and H. Wacker. 1991. The concept of sustainable yield in multi-species fisheries. *Ecological Modelling* 53:61–74.
- Ströbele, W. J., and H. Wacker. 1995. The economics of harvesting predator–prey systems. *Journal of Economics* 61:65–81.
- Swihart, R. K., Z. Feng, N. A. Slade, D. M. Mason, and T. M. Gehring. 2001. Effects of habitat destruction and resource supplementation in a predator–prey metapopulation model. *Journal of Theoretical Biology* 210:287–303.
- Thompson, G. G., Z. T. A'mar, and W. A. Palsson. 2011. Assessment of the Pacific cod stock in the Gulf of Alaska. Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, AK.
- Trites, A. W., and C. P. Donnelly. 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. *Mammal Review* 33:3–28.
- Turnock, B. J., and T. K. Wilderbuer. 2011. Assessment of the arrowtooth flounder stock in the Gulf of Alaska. Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fishery Management Council, Anchorage, AK.
- Van Kirk, K. F., T. J. Quinn, and J. S. Collie. 2010. A multispecies age-structured assessment model for the Gulf of Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1135–1148.
- Veit, R. R., E. D. Silverman, and I. Everson. 1993. Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. *Journal of Animal Ecology* 62:551–564.
- Walters, C., and J. F. Kitchell. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* 58:39–50.
- Walters, C. J., V. Christensen, S. J. Martell, and J. F. Kitchell. 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. *ICES Journal of Marine Science* 62:558–568.
- Whipple, S. J., J. S. Link, L. P. Garrison, and M. Fogarty. 2000. Models of predation and fishing mortality in aquatic ecosystems. *Fish and Fisheries* 1:22–40.
- Witherell, D., and C. Pautzke. 1997. A brief history of bycatch management measures for Eastern Bering Sea groundfish fisheries. *Marine Fisheries Review* 59:15–22.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25:443–466.
- Yodzis, P. 1994. Predator–prey theory and management of multispecies fisheries. *Ecological Applications* 4:51–58.
- Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology* 67:635–658.
- Zabel, R. W., C. J. Harvey, S. L. Katz, T. P. Good, and P. S. Levin. 2003. Ecologically sustainable yield. *American Scientist* 91:150.

SUPPLEMENTAL MATERIAL

Appendix A

Comparison of the Ricker growth model with the Beverton-Holt model ([Ecological Archives A023-050-A1](#)).

Appendix B

Non-dimensionalization of the direct-competition, predator–prey, and apparent-competition models ([Ecological Archives A023-050-A2](#)).

Appendix C

Comparison of the constant escapement harvest model with the constant-proportion model ([Ecological Archives A023-050-A3](#)).

Supplement

R code for bycatch calculations ([Ecological Archives A023-050-S1](#)).