Original Article
Evaluating the effect of a selective piscivore fishery on rockfish recovery within marine protected areas

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Although ecosystem-based fisheries management is often associated with trade-offs between conflicting demands for ecosystem services, the holistic ecological considerations the approach promotes may sometimes lead to novel solutions that benefit both conservation and fisheries. Directed fishing on large piscivorous fish can reduce predation on prey and thereby benefit those populations, but incidental take of prey species in these fisheries may negate or even reverse the benefit. Whether benefits from reduced predation outweigh the costs of increased fishing will depend on the relative strength of each mortality source and the sensitivity of the population to mortality at different life stages. In the California Current, predatory lingcod (*Ophiodon elongatus*) populations recovered rapidly from fishing exploitation over the past two decades, while recovery of some rockfish species (*Sebastes* spp.) has been slow, mainly because of low natural productivities. One management tool has been the adoption of rockfish conservation areas (RCAs) that prohibit bottom contact fishing gear. Because lingcod also inhabit RCAs, fishers have been unable to catch their sustainable lingcod quotas. Therefore, we explored the conditions under which opening RCAs to a selective lingcod fishery might permit rockfish recovery despite the potential bycatch. We developed a joint equilibrium model of the two populations and analysed scenarios to assess the sensitivity of the model's predictions to key uncertainties. The model suggests a wide range of fishery and ecological conditions under which a lingcod fishery may not harm rockfish populations. However, a sensitivity analysis indicated that the range of fishing scenarios where rockfish are not harmed is highly sensitive to assumptions regarding the nature of the trophic linkage between lingcod and rockfish. We conclude that consideration of trophic interactions may reveal new fishing opportunities that meet both ecological and human goals, but precise predictions of the outcomes will require more detailed models and adaptive management.

Keywords: age-structured model, bycatch, ecosystem-based fisheries management, marine protected areas, predator–prey dynamics, rockfish.

Introduction

There is a push in fisheries management to consider the whole social-ecological system rather than individual fish populations when making decisions and setting regulations (Levin *et al.*, 2009). This ecosystem-based approach to fisheries management acknowledges the effects of decisions on multiple interacting species and on the people who utilize such species (Arkema *et al.*, 2006). In some cases, such as forage fish management, thinking at a larger system-wide scale leads one to potentially fish less intensively than would be done using a single-species paradigm to protect predator populations (Cury *et al.*, 2011; Pikitch *et al.*, 2014). However, when there are asymmetric predator–prey interactions where the top-down effect

greatly exceeds the bottom-up effect, managers may be presented with a different set of policy choices to conserve the mid-trophic level species (Marshall *et al.*, 2016), and these choices may not necessitate less fishing overall.

One tool that has resulted from embracing a multispecies framework in the management of both aquatic and terrestrial populations is the harvest of predators to assist prey populations. Culling predators has been proposed both to increase productivity and yield of exploited prey (Flaaten and Stollery, 1996; Bowen and Lidgard, 2013) and to help conserve endangered prey species (Beamesderfer *et al.*, 1996; Williams, 2014). The basic principle of culling is that reducing predator populations reduces natural mortality rates, which in

turn increases the population growth rate (Reynolds and Tapper, 1996). When the management goal is simply to maintain the current level of population productivity, rather than to enhance it, reducing natural mortality through culling predators means that populations may be able to sustain higher harvest rates, irrespective of whether the population is a target species. However, it must be emphasized to consider that the success of culling programmes has been highly variable (Reynolds and Tapper, 1996; Bowen and Lidgard, 2013) and rests on a thorough understanding of the ecosystem in which the predator–prey interaction exists (Yodzis, 2001).

Subscribing to an ecosystem-based approach to fisheries management also includes ensuring the social and economic health of fishing communities (Arkema et al., 2006). Fishery catches can sometimes be constrained by the incidental bycatch of species of conservation concern, rather than by the amount of fishing effort that target species can sustain (Hall et al., 2000). As a result, these fisheries remain underutilized due to catch restrictions for the non-target species (O'Keefe and DeCelles, 2013). In response, technical gear modifications are often engineered that rely on behavioural or morphological differences between target and non-target species (Lomeli and Wakefield, 2012). While considering predatory and competitive interactions among species is a vital component of ecosystem-based fisheries management (Pikitch et al., 2004), so too is developing creative solutions to reduce restrictions that have arisen due to bycatch, as doing so allows us to sustain both biological communities and fishing communities alike (Graham et al., 2007).

Models can illuminate important dynamics relevant to policy development and generate new questions for future policy-relevant exploration, but it is first necessary to identify an appropriate level of model complexity for the question at hand. Simple equilibrium-based age- or stage-structured matrix models can inform management and conservation decisions by identifying key life stages sensitive to changing survival rates that warrant more conservation attention (Caswell, 2001). Age-structure is particularly important in the context of ecosystem-based fisheries management because fish often change trophic levels considerably throughout their ontogeny, serving as prey during juvenile life stages and becoming predators as adults (Scharf et al., 2000), when fish are also subject to commercial fisheries (Law, 2007; Fisher et al., 2010). However, these equilibrium matrix models generally only consider individual populations. As a result, complex whole-ecosystem models are often used instead to account for trade-offs among competing objectives and to consider indirect ecological effects resulting from management choices (Pauly et al., 2000; Fulton et al., 2011). In contrast, models of intermediate complexity that have higher resolution for only a specific component of the ecosystem can more easily and effectively answer many of these same questions, with only a minimal loss of detail (Plagányi et al., 2014). That is, simpler mathematical models continue to serve as useful conservation tools to identify influential processes, but we must advance the models so that they link dependent populations and account for both antagonistic and synergistic species interactions.

In the California Current ecosystem, many groundfish populations were depleted by overfishing that occurred in the 1980s and 1990s, leading management to establish closed fishing areas along the coast, called rockfish conservation areas (RCAs). However, not all species have been recovering at the same rate. For example, lingcod (Ophiodon elongates), a productive piscivorous species, recovered quickly once management responded (Hamel et al., 2009), whereas some of the slower growing long-lived rockfish species (Sebastes spp.) have been increasing in abundance more

gradually (PFMC, 2014). Both lingcod and rockfish occupy similar habitat on rocky reefs (Tissot et al., 2007), and juvenile rockfish are frequently found in the diets of lingcod in the San Juan Islands (Beaudreau and Essington, 2007), which lie slightly inland of the federally managed area of which the RCAs are a part. There is demand for lingcod as a target species, but the RCAs limit the development of a lingcod fishery. As a result, in 2013, fishers only caught 28% of the allowable limit for lingcod off the coasts of Washington and Oregon (Somers et al., 2014). Opening of the RCAs to a commercial lingcod fishery would likely lead to some incidental mortality of adult rockfish because of their shared habitat (Tissot et al., 2007). However, if gear, such as a trap, is sufficiently selective towards lingcod morphology and behaviour, the reduction in lingcod predation on juveniles due to the fishery's "culling" of lingcod may compensate for the incidental mortality of adult rockfish. Therefore, opening the RCAs to a lingcod fishery could lead to potential gains for fishing communities without harming the ecosystem they depend on, but there is a need to better understand the dynamics of how the rockfish and lingcod populations interact.

Here, we construct a trophically linked age-structured equilibrium-based model to explore the possible implications to rockfish populations of opening RCAs to a selective lingcod fishery. The simple equilibrium model allows for rapid evaluation of many alternative scenarios to explore under which conditions rockfish populations are most successful in ultimately attaining high abundances. While equilibrium models do not quantify recovery rates, they do quantify the long-term abundance we might expect following recovery. Thus, high abundances at equilibrium can only occur if recovery also occurs. We analyse this model under a range of fishing and ecological conditions to understand the full spectrum of possible population responses to the management change based on key uncertainties about dynamics of lingcod and rockfish. We seek to answer two main questions: (i) under what scenarios might reduced predation on juvenile rockfish compensate for the bycatch of adult rockfish by the hypothetical lingcod fishery and (ii) what model parameters are most influential in determining the answer to the first question. We acknowledge that further empirical research and modelling work will be necessary to fully evaluate a potential lingcod fishery within RCAs for implementation; here we attempt to show the fishery's theoretical plausibility and direct future research by identifying key parameters and processes that are highly uncertain, highly influential, or both, and that therefore warrant further exploration.

Methods

We constructed linked age-structured models for rockfish and lingcod and evaluated them at equilibrium conditions to calculate the level of rockfish bycatch that could be sustained in a directed lingcod fishery without reducing rockfish female spawning biomass, under a range of potential lingcod harvest intensities (Figure 1). Because of the high uncertainty in the trophic relationship between lingcod and rockfish, as well as unknown size selectivity of potential fishing gear, we use this model primarily as a platform to conduct an extensive sensitivity analysis on input parameter values to identify the conditions under which calculated equilibrium rockfish biomass is equivalent to (i) currently estimated unfished levels and (ii) the management target of 40% of the unfished biomass. We used equilibrium model conditions to permit rapid evaluation of alternative parameterizations, and thereby provide insight into how populations might respond under
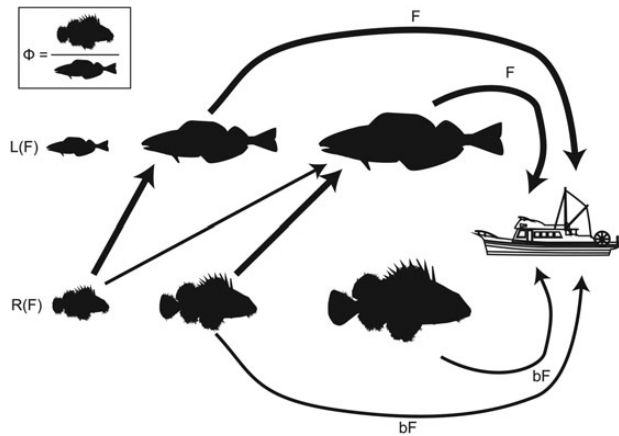
Figure 1. Model schematic. Top row represents lingcod dynamics and bottom row represents rockfish. Arrows represent mortality, either through fishing (arrow to boat) or consumption (arrow to lingcod), with widths approximating relative numbers of fish. The box in the upper left-hand corner represents the fixed recruitment ratio between the two groups, ϕ.

different conditions and illuminate key ecological and fishery parameters that can have major influence on the population dynamics.

Model structure

Because lingcod are highly opportunistic generalist predators, we assume here that lingcod predation affects rockfish populations, but that rockfish abundance does not affect lingcod population growth rates. We therefore first calculated the lingcod equilibrium properties under different fishing rates, and use that to adjust demographic parameters in an age-structured rockfish model. The initial step was to calculate the equilibrium lingcod age-structure-per-recruit in numbers-at-age. Because lingcod are highly sexually dimorphic (Hamel *et al.*, 2009), we model the two sexes explicitly and assume the sex ratio at birth is 0.5. Then $L_{a+1,s}$, the lingcod per recruit of age $a + 1$ and sex s is modelled as

$$L_{a+1,s} = L_{a,s} \exp[-(M_s^l + v_{a,s}^l F)], \quad (1)$$

where $L_{a,s}$ is the number of fish of age a and sex s, M_s the natural mortality rate of sex s, $v_{a,s}$ is the relative vulnerability to fishing gear for fish of age a and sex s, F is the mortality rate from fishing for ages that are fully vulnerable to the fishery ($v_{a,s} = 1$), and the superscript l denotes parameters that relate to lingcod. For simplicity, $v_{a,s} = 0$ or 1 (i.e. a "knife-edge" curve where each age class is either fully vulnerable or not). For the final age class, or "plus group", we divided the quantity in Equation (1) by $1 - \exp[-(M_s^l + v_{n,s}^l F)]$ where n is the plus group age (20). This process leads to a matrix of the equilibrium lingcod age-structure as a function of the fishing rate, $L(F)$.

The rockfish population model only includes females, as females generally determine a fish population's ability to persist (Hixon *et al.*, 2014). Lingcod consumption was halved to adjust for this simplification. We calculated the equilibrium female rockfish age-structure scaled to lingcod recruitment by fixing the ratio of recruitment between the two groups. Then apply a similar equation as above:

$$R_{a+1} = R_a \exp[-(M^r + v_a^r bF)] - Q_a(L, R, F), \quad (2)$$

where $R_1 = \phi/2$ and ϕ is the ratio of rockfish recruits to lingcod recruits, the r superscript denotes parameters that relate to rockfish, and Q_a is the consumption of age a rockfish per lingcod recruit. We define this vector as $R(F)$. The variable b is the gear selectivity efficiency, or, more explicitly, the fraction of lingcod fishing mortality that fully selected rockfish experience; it describes how effectively the fishing gear avoids rockfish. When $b = 1$, the mortality rates of rockfish and lingcod are equal, implying that the gear is indiscriminate between groups. For well-constructed gear, $b \ll 1$. For the plus group, age class n, Equation (2) becomes

$$R_n = \frac{R_{n-1} \exp[-(M^r + v_{n-1}^r bF)] - Q_{n-1}(L, R) - Q_n(L, R)}{1 - \exp[-(M^r + v_n^r bF)]}. \quad (3)$$

Equations 2 and 3 assume that populations are not subject to any other fishing mortality; that is, they are closed populations within no-take marine reserves. Also, they presume that mortality from lingcod occurs after other natural mortality and after fishing. A scenario with constant recruitment that is independent of spawning biomass explored sensitivity to the assumption that populations are closed. Sensitivity to the assumption regarding the order of mortality was tested using numerical methods, and results were nearly indistinguishable between the model with lingcod mortality occurring after other mortality sources and the model with all mortality occurring simultaneously. We then calculated total rockfish spawning biomass per rockfish recruit to use in a stock–recruit function and ultimately evaluate the impact of lingcod fishing on rockfish populations. We calculated this as $[R(F)'W^r]/(\phi/2)$. Here, W^r is a vector of rockfish weights-at-age, and the apostrophe denotes the transpose of a vector.

We needed to account for size-selective vulnerability of rockfish for each age class of lingcod, using existing information on prey size spectra of lingcod. To do this, each age class of lingcod for both sexes was assumed to have a diet size spectrum that was represented by a unique gamma probability distribution with quantiles that increased linearly with lingcod size. These distributions were integrated over length bins determined by the length-at-age of each rockfish age class (see Supplementary Materials for equation). This assigned the relative vulnerability of each age class of rockfish to predation by each age and sex of lingcod. The area in each length bin was normalized so that the sum over all rockfish age bins was one. We then used the probabilities from these bins to populate an array D that gives the preference of lingcod of each age and sex to consume rockfish of each age, relative to the lingcod's overall preference to consume rockfish. In this way, D is an array of two $r \times l$ matrices (one for each lingcod sex) where r is the number of rockfish age classes and l is the number of lingcod age classes, and each column of D sums to one. For details, see Supplementary Materials.

We calculated lingcod consumption of rockfish, $Q(R, L)$, using two distinct functional responses that represent two endpoint scenarios. The first was where the lingcod per capita consumption was independent of rockfish density (heretofore referred to as "saturating"). The second was a linearly increasing response, where lingcod per capita consumption is directly proportional to rockfish density (i.e. Hollings type I). These two simple cases bracket a range of other more complex and realistic lingcod consumption patterns, but we expect results from those cases to fall intermediate to our two endpoints. For the simpler method with a saturating response, we define P as a vector that represents the proportion of lingcod consumption that is composed of rockfish, by lingcod age, and define C as a matrix

of total lingcod annual per capita consumption by lingcod age and sex. Then to calculate consumption of rockfish per lingcod recruit, Q, we calculate:

$$Q_{a_r} = \frac{\sum_s \sum_{a_l=0}^{l} D_{a_r,a_l,s} \, 0.5 \, C_{a_l,s} \, P_{a_l} L_{a_l,s}(F)}{W_{a_r}^r} \,, \tag{4}$$

where the subscript s denotes sex, the division is elementwise, and the one-half appears to account for consumption of female rockfish only. The result of Equation (4) is a vector with r elements, one for each rockfish age class.

For the type I functional response where lingcod diets adapt to changing rockfish abundances, we needed to adopt a separate functional response for each combination of lingcod and rockfish age classes. We assumed the per capita consumption of rockfish increases linearly with rockfish abundance at each rockfish age class (per lingcod recruit). To set the slope of this relationship, we assumed that, when summed over all rockfish age classes, the total per capita consumption passes through the origin and is equal to the value at the saturating functional response when rockfish are at the unfished biomass. In addition, lingcod preference towards each rockfish age class was weighted by the diet size spectra. We therefore assumed that

$$Q_{a_r} = R_{a_r}(F) \sum_s \sum_{a_l=0}^{l} \frac{D_{a_r,a_l,s} \, 0.5 \, C_{a_l,s} \, P_{a_l} L_{a_l,s}(F)}{\sum_{i=0}^{r} D_{i,a_l,s} R_i(0) W_i}, \tag{5}$$

where w_a^r is the weight of age a rockfish. In this case, the vector Q must be calculated sequentially for each rockfish age class, and cannot be done in a single calculation as in (4). In addition, the unfished condition, $R(0)$, must be calculated numerically by solving a system of non-linear equations. To accomplish this, we used the package nleqslv in R (Hasselman, 2015). For a derivation of Equation (5), see Supplementary Materials. Note that P now represents the diet proportions at the unfished biomass. The actual diet proportion now scales with the rockfish population. However, the values within P remain unchanged.

To examine different levels of density dependence in the stock–recruit relationship, we examined rockfish spawning biomass instead of rockfish spawners-per-recruit. Because we fixed the ratio of recruitment between the two groups, there is only one free stock–recruit relationship between the two species groups. We briefly tested sensitivity to this assumption (see Supplementary Materials), but in general keep the constant ratio because it allows us to calculate the equilibria analytically and therefore explore model outcomes over a wide range of parameters and scenarios. We varied rockfish density-dependence through the steepness parameter (h) in the Beverton–Holt stock–recruit relationship. A steepness of one indicates that recruitment is independent of spawning biomass, and a steepness of 0.2 indicates density-independent per capita recruitment. We fixed the unfished recruitment to one always, as this simply scales the size of both populations, but does not influence dynamics of the system. We calculated rockfish female spawning-stock biomass (*SSB*) from spawners–per–recruit (R) using the following formula:

$$SSB(F) = \frac{4hR(F) - (1-h)R(0)}{5h - 1}. \tag{6}$$

Baseline parameterization

Demographic parameters (Table 1) were obtained from the most recent stock assessments for lingcod (Hamel *et al.*, 2009) and yelloweye rockfish (Taylor and Wetzel, 2011). Yelloweye rockfish (*Sebastes ruberrimus*) is an overfished rockfish species with major habitat overlap with lingcod (Tissot *et al.*, 2007), and with similar demographic characteristics to other slow-growing rockfish species, such as canary rockfish (*Sebastes pinniger*). For both lingcod and rockfish, total length-at-age, S_a, was modelled with a parameterization of the von Bertalanffy growth function:

$$S_a = S_\infty - (S_\infty - S_1) \exp[-K(a - 1)], \tag{7}$$

where S_∞ is the asymptotic length, S_1 is the length-at-age 1, and K is the growth rate parameter. For lingcod, this relationship was sex specific. For rockfish, we decreased the length of the youngest age class to 10 cm, as these young rockfish are particularly vulnerable to predators and their size is not well estimated in the stock assessment because there are no data to inform it. Rockfish weight-at-age was taken directly from the age-structured stock assessment, which models weight in kilograms as an allometric scaling of length (Supplementary Table S1). Because we are partitioning rockfish natural mortality into lingcod and non-lingcod sources, the overall stock assessment natural mortality rate would overestimate M^r, which we assume to come from non-lingcod sources only. Therefore, non-lingcod natural mortality of rockfish was set to 0.043 years^{-1}, so that the weighted average of total natural mortality over ages 10 and above under the baseline scenario would be approximately equal to the total natural mortality rate used in the stock assessment (0.046). Age 10 was chosen as the cutoff because that is the age at which most stock assessment indices of abundance have $>50\%$ selectivity (Taylor and Wetzel, 2011). Lingcod consumption rates are based on Beaudreau and Essington (2009), then corrected using their reported Q_{10} temperature coefficient of 1.9 for the lower temperatures found on the continental shelf when compared with Puget Sound (6 vs. 9°C). The function for lingcod consumption for sex s, measured in kilograms per capita per year, was

$$C = a_{c,s} W^{b_{c,s}}, \tag{9}$$

where weight-at-age in kilograms for lingcod was calculated using the allometric scaling of length-at-age $a_{w,s} S^{b_{w,s}}$.

Remaining model parameters were known with considerable uncertainty, and form the basis for the extensive sensitivity analysis that followed model construction. However, baseline values were selected. Lingcod were considered vulnerable to the fishery at 60 cm, which is near 50% selectivity for the commercial trawl fishery (Hamel *et al.*, 2009). Rockfish were considered vulnerable at 25 cm, a smaller size than the lingcod, because we assume fish are captured by the gear at 25 cm, and, unlike lingcod, no captured rockfish survive due to barotrauma (Parker *et al.*, 2006). This is somewhat close to the inflection point of yelloweye selectivity curves in Washington, which is ~40 cm for both the trawl and recreational fisheries (Taylor and Wetzel, 2011); note that there is currently no trap fishery for rockfish. The lingcod diet size spectra are gamma distributions where the fifth and 95th quantiles increase linearly with lingcod size (Figure 2). The slopes of these two quantiles define the size spectra. Baseline slopes are from the total lingcod diet

Table 1. Model parameters.

Symbol	Name	Value	Source
$S^l_{\infty,m}$	Maximum length—male lingcod	86.9 cm	Hamel *et al.* (2009)
$S^l_{\infty,f}$	Maximum length—female lingcod	126.3 cm	Hamel *et al.* (2009)
$S^l_{1,m}$	Length-at-age 1—male lingcod	29.7 cm	Hamel *et al.* (2009)
$S^l_{1,f}$	Length-at-age 1—female lingcod	28.1 cm	Hamel *et al.* (2009)
K^l_m	von Bertalanffy K—male lingcod	0.22 years^{-1}	Hamel *et al.* (2009)
K^l_f	von Bertalanffy K—female lingcod	0.13 years^{-1}	Hamel *et al.* (2009)
$a^l_{w,m}$	Weight–length intercept—male lingcod	3.953E−6 kg/cm^{b_w}	Hamel *et al.* (2009)
$a^l_{w,f}$	Weight–length intercept—female lingcod	1.76E−6 kg/cm^{b_w}	Hamel *et al.* (2009)
$b^l_{w,m}$	Weight–length exponent—male lingcod	3.2149	Hamel *et al.* (2009)
$b^l_{w,f}$	Weight–length exponent—female lingcod	3.3978	Hamel *et al.* (2009)
M^l_m	Natural mortality—male lingcod	0.32 years^{-1}	Hamel *et al.* (2009)
M^l_f	Natural mortality—female lingcod	0.18 years^{-1}	Hamel *et al.* (2009)
h^l	Steepness of lingcod Beverton–Holt relationship	0.8	Hamel *et al.* (2009)
S^r_∞	Maximum length—rockfish	63.9 cm	Taylor and Wetzel (2011)
S^r_1	Length-at-age 1—rockfish	18.4 cm	Taylor and Wetzel (2011)
K^r	von Bertalanffy K—rockfish	0.049 years^{-1}	Taylor and Wetzel (2011)
a^r_w	Weight–length intercept—rockfish	9.77E−6	Taylor and Wetzel (2011)
b^r_w	Weight–length exponent—rockfish	3.17	Taylor and Wetzel (2011)
M^r	Non-lingcod rockfish natural mortality	0.043 years^{-1}	Taylor and Wetzel (2011)
h^r	Steepness of rockfish Beverton–Holt relationship	0.441, 1	Taylor and Wetzel (2011)
$a_{c,m}$	Lingcod consumption intercept—males	3.01	Beaudreau and Essington (2009)
$a_{c,f}$	Lingcod consumption intercept—females	3.31	Beaudreau and Essington (2009)
$b_{c,m}$	Lingcod consumption exponent—males	0.75	Beaudreau and Essington (2009)
$b_{c,f}$	Lingcod consumption exponent—females	0.77	Beaudreau and Essington (2009)
P_{6+}	Rockfish diet proportion for lingcod ages 6+	0.01, 0.02, **0.03**, 0.04	Koehn *et al.* (unpublished)
ϕ	Rockfish:lingcod recruitment ratio	11.4, 22.4, 33.4, 44.4, 55.2	Kaplan *et al.* (2014)
ML^l	Minimum length caught by fishery—lingcod	40, 50, **60**, 70 cm	Hamel et al. (2009)
ML^r	Minimum length caught by fishery—rockfish	20, **25**, 30, 35 cm	Taylor and Wetzel (2011)
γ_5	Slope of fifth quantize of diet size spectra	0.05	Beaudreau and Essington (2007)
γ_{95}	Slope of 95th quantile of diet size spectra	0.27, **0.29**, 0.31, 0.33	Beaudreau and Essington (2007)

When multiple values were explored for a single parameter, bold indicates the "baseline" scenario used.
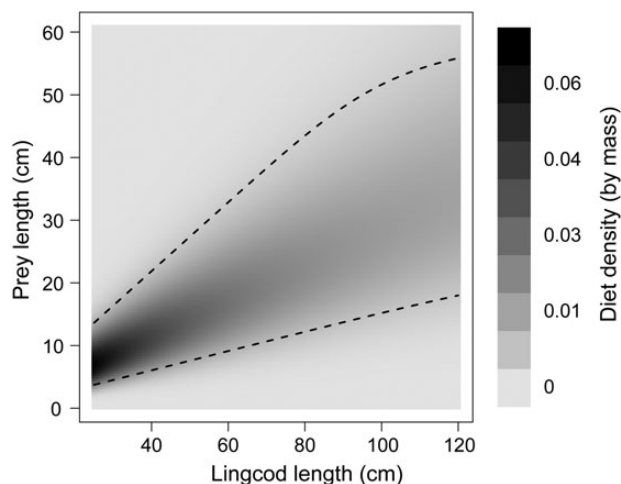

Figure 2. Size spectra of lingcod diets in the base case model. Each vertical slice is a probability distribution of the diet size spectrum for a given lingcod size. Darker colours indicate higher probability density. Dashed lines represent the fifth and 95th percentiles. Adapted from Beaudreau and Essington (2007).

described by Beaudreau and Essington (2007). All reported slopes are with respect to standard length for rockfish, which were obtained from total lengths based on Echeverria and Lenarz (1984). The recruitment ratio, ϕ, was tuned so that the ratio of unfished biomasses

of demersal rockfish species to lingcod approximately matched the ratio in the California Current (Kaplan *et al.*, 2014). The rockfish diet fraction of adult lingcod, *P*, was approximately based on a California Current mass-balance model (Koehn *et al.*, unpublished). While our model is parameterized for large slow-growing rockfish species, we assume that their relative abundance within the rockfish guild is similar to their relative abundance within the rockfish component of lingcod diets, so that using information on the whole rockfish clade is a reasonable simplification. However, the large slow-growing rockfish modelled here likely make up a smaller fraction of lingcod diets than their relative abundance among all rockfish, as some rockfish remain small their entire lives. Therefore, in the baseline model, we used a slightly (one percentage point) smaller diet proportion than Koehn *et al.* (unpublished), then explored a range of possible values. In addition, the diet proportion was assumed to increase linearly for the first six lingcod ages modelled, beginning at 0, as young lingcod likely eat relatively less rockfish than older lingcod.

The full set of parameters explored is listed in Table 1. The model was built and analysed in R version 3.1.1 (R Core Team, 2014).

Results

The different parameterizations consistently show that when fishing is conducted at low enough intensities and with minimal incidental catch of rockfish, opening marine protected areas to a selective lingcod fishery (i.e. low gear selectivity efficiency) may actually enhance equilibrium population levels of vulnerable rockfish populations (Figure 3), indicating that populations will ultimately
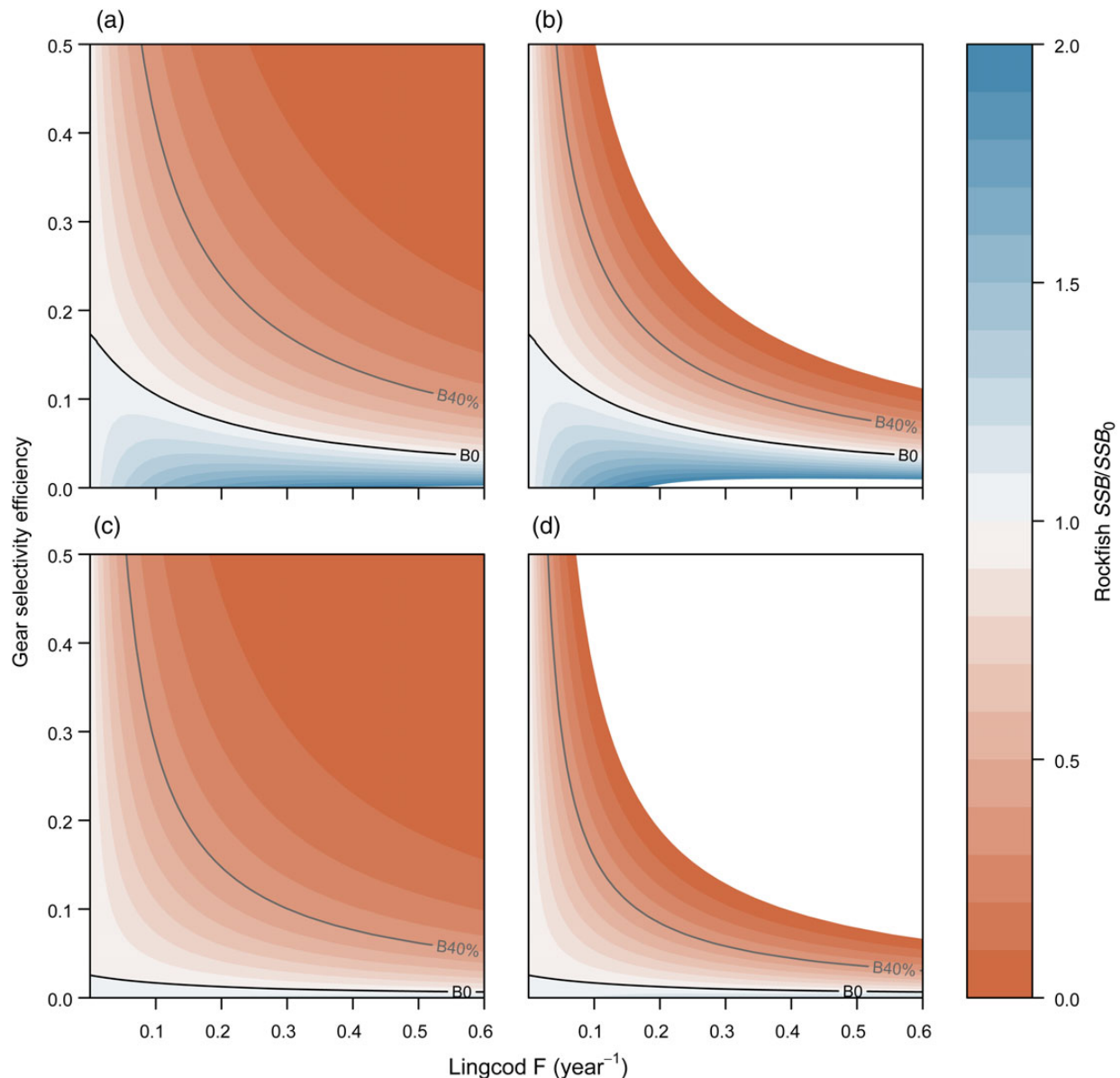
Figure 3. Effect of density-dependence and functional response on the rockfish *SSB* response to a potential lingcod fishery, when compared with unfished rockfish levels (SSB_0). Panels (a and b) assume a constant fraction of lingcod diets composed of rockfish (saturating response) whereas (c and d) include a type I functional response. Panels (a and c) have constant recruitment, whereas (b and d) have a Beverton–Holt steepness for rockfish of 0.441. The contour line "B0" marks where rockfish biomass remains at the unfished level. The "B40%" contour marks where rockfish biomass remains at the management target of 40% of the unfished level. Gear selectivity efficiency (represented by *b* in equations) is the fraction of lingcod fishing mortality that rockfish experience, and indicates how effectively the gear selects against rockfish. It ranges from 0 (perfectly selective gear, zero rockfish bycatch) to 1 (indiscriminant gear, unbiased between lingcod and rockfish). This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

recover to higher levels. Equilibrium biomass is maintained at the level it will eventually reach in the absence of fishing along a contour line defined by lingcod fishing intensity and relative gear selectivity for the two species. The maintenance line curves downwards, indicating that rockfish biomass levels would be unchanged by either high fishing effort with low bycatch or with low harvest intensity and less selective fishing gear. In other words, to increase fishing effort while also sustaining rockfish populations in the long term, it is necessary to improve species selectivity of the lingcod fishing gear. However, the relationship is non-linear; incrementally increasing fishing intensity when effort is low requires

a larger improvement in gear than undergoing the same incremental increase while fishing efforts are already high. The fishing mortality that leads to maximum sustainable yield for lingcod is 0.15 years^{-1} (Hamel *et al.*, 2009), which intersects the unfished contour at a gear selectivity efficiency of 0.08. Thus under the base case of our model, lingcod populations can be fully utilized while maintaining eventual equilibrium rockfish populations at unfished levels if rockfish fully-selected fishing mortality remains <0.004 years^{-1} (the product of 0.15 and 0.08), and there is no other rockfish harvest.

Away from the unfished rockfish biomass, the isoclines for biomasses that are greater than the unfished level are not monotonic

(Figure 3). This is because there are actually two contours where equilibrium rockfish biomass is equal to the unfished level: (i) the downwards sloping curve that is plotted in black and (ii) the *y*-axis, where fishing mortality is zero and populations are by definition unfished. Contour lines for different relative biomasses cannot intersect, so the lines for the higher biomass levels must curve downwards instead of intersecting the *y*-axis. Essentially, when the fishing gear selects almost perfectly for lingcod, increasing fishing intensity at low levels decreases predation mortality more than it increases fishing mortality, and rockfish populations actually benefit. For biomasses above the unfished level, there is an extremely small range of low fishing intensities where rockfish biomass can be maintained at a constant level by increasing the fishing intensity and making less selective gear. However, target levels in the California Current are 40% of the unfished biomass, and populations are currently well below that target.

The stock–recruit relationship, or amount of density dependence, has no bearing on the unfished rockfish biomass contour, but does influence how the equilibrium rockfish spawning biomass changes as fishing conditions move away from those that result in unfished biomass (Figure 3a,c vs. b,c). Recruitment at the unfished rockfish biomass is defined to be the same for the two relationships; recruitment only differs at other biomasses. A highly density-dependent population (i.e. steepness ∼1, recruitment is constant) is more resilient and maintains a biomass near the unfished level under a wide range of fishing conditions because recruitment to the population remains high even when spawning biomass is low. With less density-dependence (i.e. steepness $\ll$1), fishing can greatly reduce (or increase) the rockfish population's reproduction rate, leading to larger changes in equilibrium spawning biomass resulting from more incremental shifts in fishing conditions. This occurs because recruitment responds strongly to changes in spawning biomass caused by fishing. Understanding the stock–recruit relationship therefore has important implications for management targets, which are set at 40% of the unfished biomass. If the population displays high density dependence, there is a wider range of fishing scenarios that will lead to rockfish biomasses at or above target levels.

Including a functional response where lingcod eat more rockfish when rockfish are more abundant leads to major differences, particularly at low fishing efforts ($F <$ ca. 0.2), in both the unfished biomass contour and the entire rockfish spawning biomass surface (Figure 3c, d vs. a, b). Although the model assumes that lingcod consume the same mass of rockfish in the absence of fishing for both scenarios, the age-structure of the consumed rockfish differs. Under the saturating functional response, lingcod eat large masses of juvenile rockfish, which are of optimal size, though not necessarily abundant. When the lingcod respond to relative rockfish abundance, the lingcod consume more large rockfish despite their suboptimal size. Therefore, under the saturating functional response, fishing lingcod better improves survival probabilities for the small juvenile rockfish that are crucial to population growth. However, it is notable that the total unfished rockfish spawning biomass is approximately three times greater with the type I functional response because fewer individuals are consumed in this case, thus resulting in a lower natural mortality rate. For simplicity, remaining results from the sensitivity analysis are presented assuming a saturating functional response, but only the unfished biomass contour is examined. Behaviour away from the unfished contour showed similar tendencies to the base case, and including a type I functional response produced similar changes to those described above.

The model was highly sensitive to changes in parameters related to how much rockfish lingcod consume (diet fractions and size spectra, Figure 4a and b). When rockfish comprise a larger fraction of lingod diets, lingcod fishing has a greater benefit to rockfish. Therefore, fishing lingcod while maintaining a constant species selectivity of the gear is more likely to have neutral to positive impacts on rockfish populations when lingcod consume high volumes of rockfish. Increasing the slope of the 95th quantile of the gamma distribution for lingcod diet size spectra led to a larger area where rockfish populations decline. Increasing these slopes generally increases the average size of rockfish that lingcod consume. Lingcod have a larger impact on rockfish, and thus rockfish are less likely to be harmed by a lingcod fishery, when lingcod select younger smaller fish because those fish have not yet had many opportunities to reproduce. Rockfish populations are sensitive to changes in juvenile survival. Therefore, in cases where lingcod strictly eat smaller rockfish, the benefits to rockfish of the lingcod fishery (predator culling) are more likely to outweigh the costs (bycatch).

The sensitivity analysis showed that while varying size selectivity of the fishing gear on both rockfish and lingcod does influence rockfish biomass, the changes in the unfished biomass contour are small, implying that size selectivity of fishing gear need only be known approximately to understand impacts of the potential fishery on rockfish populations (Figure 5). Results demonstrated that selecting a wider range of lingcod sizes tends to slightly benefit the rockfish populations, as doing so results in removing more potential predators from the water, essentially increasing the fishing effort (Figure 5a). However, such a change in the fishing gear would likely increase the range of rockfish sizes selected, as well, which would hamper rockfish recovery (Figure 5b).

Changing the ratio of recruitment (and therefore total abundance) between rockfish and lingcod led to less dramatic changes than altering diets, but more substantial changes in rockfish dynamics than shifting gear selectivity (Figure 4c). It is also notable that the unfished contour line moves more as the relative abundance of lingcod increases. Although the current ratio of demersal rockfish to lingcod biomass is ca.. 9 (Kaplan *et al.*, 2014), the analysis here explores dynamics of the unfished system, where rockfish are fully recovered, and the ratio is thus likely to be greater. Decreasing the relative abundance of lingcod in the system decreases the range of scenarios where rockfish populations would benefit from the lingcod fishery due to reduced predation (i.e. the contour line falls at lower fishing mortality rates and gear selectivity efficiencies indicating more selective gear). This is because the fishery removes fewer rockfish predators when rockfish are more relatively abundant. As the per capita rockfish consumption is constant, there is no compensation in rockfish consumption at high lingcod densities.

Discussion

We explored the effects on rockfish of establishing a selective commercial lingcod fishery within rockfish conservation areas (RCAs) that currently restrict fishing of groundfish to protect sensitive rockfish populations and enhance their recovery. To do this, we constructed an equilibrium-based age-structured model that links rockfish abundance to their lingcod predators. We found that the fishery could avoid harming rockfish populations under a range of conditions, even with some levels of rockfish bycatch. The effect of a selective lingcod fishery on rockfish populations depends extensively on the consumption habits of lingcod; the fishery is least likely to harm rockfish when lingcod eat a large
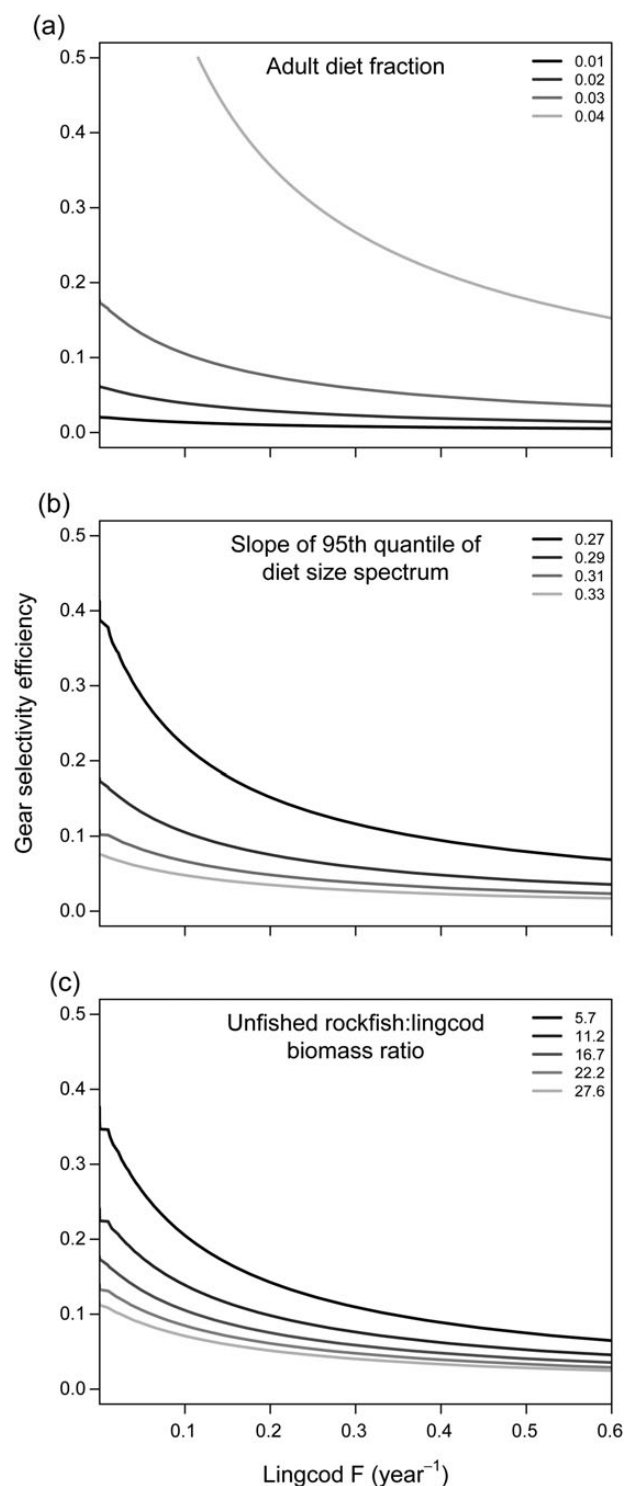
Figure 4. Sensitivity analysis to input model parameters. Lines represent the contour over which rockfish populations equilibrate at unfished spawning biomass. The lower the contour line, the greater the area of the plotted parameter space where equilibrium rockfish populations are below unfished biomass. The biomass ratio levels (c) are based on changing the recruitment ratio of rockfish to lingcod; however, biomass is reported for interpretation.
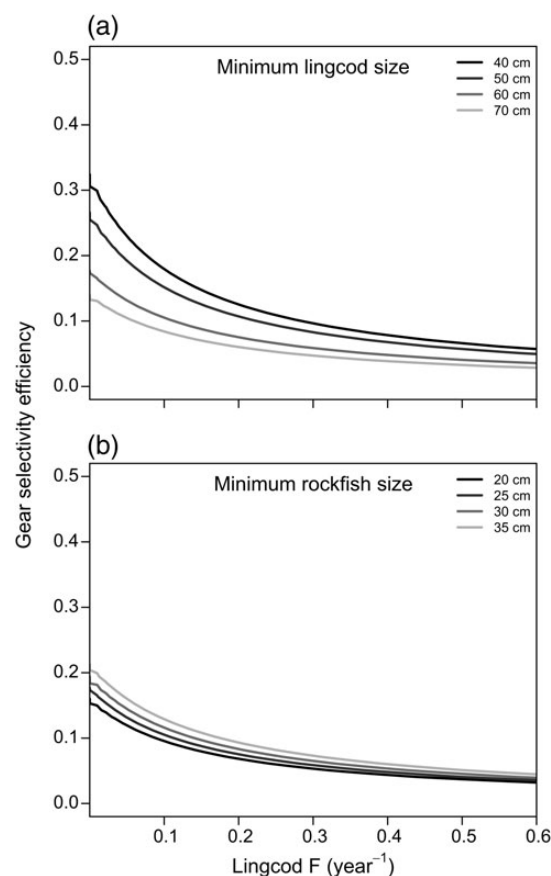

Figure 5. Sensitivity analysis to fishery size selectivity. Lines represent the contour over which rockfish populations equilibrate at unfished spawning biomass. The lower the contour line, the greater the area of the plotted parameter space where equilibrium rockfish populations are below unfished biomass.

gear testing, and experimental application may be warranted if conducted in a careful and adaptive manner. In general, this work illustrates that ecosystem-based fishery management does not always necessitate trade-offs and tighter fishing quotas, but rather it recognizes connections among species and can lead to novel solutions that benefit both fisheries and overfished species. Although culling predators can sometimes lead to unexpected ecological outcomes (Punt and Butterworth, 1995; Yodzis, 2001), passive policies that restrict harvest of a protected species but do not additionally control predator abundances are sometimes less effective at restoring populations (Lessard et al., 2005; Baskett et al., 2006). Therefore, taking a flexible and creative approach towards MPAs and allowing for the harvest of abundant and productive predator species could be a socially, economically, and ecologically sustainable policy.

This work corroborates results from previous mathematical models involving rockfish and MPAs in the California Current, which generally found that considering community dynamics (both competition and predation) had a significant impact on the predicted ecological responses to management practices. (Mangel and Levin, 2005; Baskett et al., 2006). Mangel and Levin (2005) found that considering community dynamics, specifically the predator–prey interaction between rockfish and lingcod, led to a completely different decision on the optimal location to place the marine reserve. We further explore the predator-prey relationship

quantity of small rockfish. However, this study only serves as an initial starting point; further exploration and model development,

with show that its consideration should affect the regulations surrounding the MPA, not only its location. Baskett *et al.* (2006) found that the populations of larger species such as yelloweye may not recover to previous levels in the mere absence of fishing due to changes in foodweb interactions that result from the MPA, although since then some species have made complete recoveries, at least over large spatial scales (PFMC, 2014). In our case, the highly abundant lingcod populations could possibly be preventing rockfish recovery, though an explicit analysis of rebuilding times is beyond the scope of this work. However, decreasing predation by lingcod *without* harvesting rockfish may improve the chances that yelloweye recover to levels that are deemed to be above safe biological limits.

We extended these previous mathematical models by incorporating an explicit and detailed age-structure. The rockfish population of conservation concern in previous work was divided into juveniles and adults, but the second species (lingcod or small rockfish) was modelled as a single homogeneous population (Mangel and Levin, 2005; Baskett *et al.*, 2006). Size structure is important in accurately modelling competition and predation among fish because of the ontogenetic shifts these species undergo (Scharf *et al.*, 2000). Our finely detailed age-structure of both species of interest was crucial, as small changes in the diet size spectra of lingcod led to large qualitative shifts in model behaviour, and therefore potentially sustainable levels of fishing effort. We would not have realized the importance of understanding the size distribution of lingcod diets, in addition to diet quantity, without this level of detail. Also, including explicit size structure of both rockfish and lingcod allowed us to show the robustness of our results to the age selectivity of fishing gear, and illustrated the opposite effects that changing the size of fish selected by the gear has on rockfish and lingcod.

Spatial management strategies, such as the implementations of MPAs, are valuable tools in ocean conservation, and can even increase fishery productivity (Gell and Roberts, 2003; Lester *et al.*, 2009), but need to be used thoughtfully because blanket fishing area closures are often met with pushback from local communities (Agardy *et al.*, 2003). Extensive research shows that the optimal configuration of MPAs depends on fish movement and dispersal (Botsford *et al.*, 2003) and the purpose of the MPA: biodiversity vs. fishery yield (Hastings and Botsford, 2003). However, community ecology is also an important factor in setting regulations for MPAs (Gerber *et al.*, 2003). Species interactions are sometimes seen as an impetus to increase the necessary size of MPAs (Walters, 2000), but rarely to alter the fishing regulations. This work illustrates the importance of beginning with the management goal, such as rockfish recovery, rather than simply applying the tool without considering the complex foodweb that exists within a proposed MPA. Both the ecosystem and associated fishing communities can benefit from MPAs when they are flexible so that fishing restrictions are tailored to the system and regulations are motivated by the local ecology (Agardy *et al.*, 2003).

We found that the model was most sensitive to parameters that influence how much rockfish lingcod consume, a similar result to sensitivity analyses from multispecies age-structured stock assessments (Van Kirk *et al.*, 2015). This work showed the particular value in gaining more quantitative information on species interactions, particularly amidst the growing chorus calling for multispecies fisheries management (Pikitch *et al.*, 2004). Diet patterns generally shift through space and time as abundances of different prey species ebb and flow (Link and Garrison, 2002). Therefore,

longer time series of diets over larger spatial scales than are currently available that include sizes of both predators and prey would help elucidate trophic relationships (Szoboszlai *et al.*, 2015). Although improving precision substantially may involve collecting prohibitively large numbers of lingcod stomachs, collecting lingcod stomachs directly from a potential fishery could in fact provide an opportunity for adaptive management. In addition, because lingcod are opportunistic generalists, their diets often simply sample whatever prey assemblages are present (Link, 2004). Therefore, a more quantitative understanding of the overlap of habitat preferences between lingcod and rockfish would also help inform management (Tissot *et al.*, 2007).

This study represents an initial exploration into the potential to open RCAs in the California Current to a selective lingcod fishery, but as with any modelling exercise, many ecological assumptions were made that may increase optimism towards the fishery. Both rockfish and lingcod shift habitat preferences as they grow, often moving from the nearshore to the offshore environments (Love *et al.*, 2002; Hamel *et al.*, 2009). Therefore, the relative abundance of juvenile rockfish in adult lingcod diets may actually be less than the relative abundance of juveniles among all benthic rockfish, although submersible surveys have shown major habitat overlap between adult lingcod and both juvenile and adult rockfish (Tissot *et al.*, 2007). This would bias our results towards finding that a potential lingcod fishery is more sustainable for rockfish than is actually true, because lingcod are able to influence rockfish dynamics more when their consumption is more targeted towards juveniles. In addition, the large-bodied rockfish modelled here engage in more anti-predator behaviour than shorter-lived species (Frid *et al.*, 2012), which would result in large rockfish species being less prevalent in lingcod diets than expected, similarly biasing the results. We are hopeful that the range of diet fractions and relative abundances of rockfish and lingcod examined in the sensitivity analysis encompass actual conditions. Second, our model does not include other ecological interactions, like cannibalism in lingcod or competition of rockfish with other mesopredators, such as gadids, that may be released by lower lingcod abundances. If increased competition with mesopredators (including juvenile lingcod) effectively replaces decreased lingcod predation, rockfish would be more sensitive to the lingcod fishery (Lessard *et al.*, 2005). Increasing mesopredator populations could also cascade to lower trophic levels, decreasing abundance of their prey such as shrimp (Frid and Marliave, 2010), and therefore decreasing rockfish productivity. Although our model does not perfectly represent reality, and these assumptions are likely to impact the absolute rockfish response, the assumptions are less likely to affect the response of rockfish relative to other scenarios tested (i.e. the sensitivity analysis).

We also made several mathematical simplifications that do not necessarily bias our results, but do influence how they should be interpreted. First, many of the individual parameters tested likely co-vary. For example, a higher rockfish to lingcod recruitment ratio likely means that rockfish comprise a larger fraction of lingcod diets, as well. Because of this, we did not extend our sensitivity analysis to more extreme values, such as different orders of magnitude. Varying individual parameters allows us to more precisely understand the effect of each process, but we acknowledge that some realism is lost. Second, we undertook a simple equilibrium analysis although rockfish are still recovering from an overfished state, and transient dynamics can dominate for decades after the establishment of MPAs (White *et al.*, 2013). Equilibrium analyses

are useful because they are generally easy to compute, allowing for the rapid initial evaluation of many different scenarios. However, population recovery necessarily occurs during periods of transience, and whether any ecosystem ever truly reaches a "stable" equilibrium is questionable (Simberloff, 1974). Even so, equilibrium analyses serve as important exploratory tools to begin to analyse recovery dynamics; their rapid evaluation can help to identify key parameters and general patterns that hold across many different possible situations.

Admittedly, yelloweye rockfish will always be a relatively rare species, and identifying stomach contents beyond the rockfish genus is challenging (Love *et al.*, 2002). Therefore, gaining a true understanding of the spatial intricacies concerning how lingcod consume relatively rare rockfish species will be challenging. Without more detailed knowledge about the strength of the trophic relationship between rockfish and lingcod and their place in the ecosystem, any potential fishery should be examined and established under conservative precautionary assumptions (Lauck *et al.*, 1998). This means assuming lower lingcod consumption rates over a wide range of rockfish sizes and smaller fractions of lingcod diets that are rockfish. A full management strategy evaluation accounting for uncertainty in the "state of nature" that is lingcod consumption could help quantify the amount of risk managers assume by allowing for the lingcod fishery (Smith *et al.*, 1999), and results from this current study could help to inform such an analysis. However, uncertainty in possible outcomes must also be weighed against the possible benefits to the entire social-ecological system. Despite uncertainty, these preliminary models indicate that the foodweb in the California Current may offer a unique policy opportunity where fishing communities can benefit beyond the status quo while also sustaining the biological community.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

References

Agardy, T., Bridgewater, P., Crosby, M. P., Day, J., Dayton, P. K., Kenchington, R., Laffoley, D., *et al.* 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. Aquatic Conservation: Marine and Freshwater Ecosystems, 13: 353–367.

Arkema, K. K., Abramson, S. C., and Dewsbury, B. M. 2006. Marine ecosystem-based management: from characterization to implementation. Frontiers in Ecology and the Environment, 4: 525–532.

Baskett, M. L., Yoklavich, M., and Love, M. S. 2006. Predation, competition, and the recovery of overexploited fish stocks in marine reserves. Canadian Journal of Fisheries and Aquatic Sciences, 63: 1214–1229.

Beamesderfer, R. C., Ward, D. L., and Nigro, A. A. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (Ptychocheilus oregonensis) in the Columbia and Snake rivers. Canadian Journal of Fisheries and Aquatic Sciences, 53: 2898–2908.

Beaudreau, A. H., and Essington, T. E. 2007. Spatial, temporal, and ontogenetic patterns of predation on rockfishes by lingcod. Transactions of the American Fisheries Society, 136: 1438–1452.

Beaudreau, A. H., and Essington, T. E. 2009. Development of a new field-based approach for estimating consumption rates of fishes and comparison with a bioenergetics model for lingcod (Ophiodon elongatus). Canadian Journal of Fisheries and Aquatic Sciences, 66: 565–578.

Botsford, L. W., Micheli, F., and Hastings, A. 2003. Principles for the design of marine reserves. Ecological Applications, 13: 25–31.

Bowen, W. D., and Lidgard, D. 2013. Marine mammal culling programs: review of effects on predator and prey populations. Mammal Review, 43: 207–220.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, MA.

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J., Furness, R. W., Mills, J. A., *et al.* 2011. Global seabird response to forage fish depletion—one-third for the birds. Science, 334: 1703–1706.

Echeverria, T., and Lenarz, W. 1984. Conversions between total, fork, and standard lengths in 35 species of sebastes from California. Fishery Bulletin, 82: 249–251.

Fisher, J. A. D., Frank, K. T., and Leggett, W. C. 2010. Breaking Bergmann's rule: truncation of Northwest Atlantic marine fish body sizes. Ecology, 91: 2499–2505.

Flaaten, O., and Stollery, K. 1996. The economic costs of biological predation. Environmental and Resource Economics, 8: 75–95.

Frid, A., and Marliave, J. 2010. Predatory fishes affect trophic cascades and apparent competition in temperate reefs. Biology Letters, 6: 533–536.

Frid, A., Marliave, J., and Heithaus, M. R. 2012. Interspecific variation in life history relates to antipredator decisions by marine mesopredators on temperate reefs. PLoS ONE, 7: e40083.

Fulton, E. A., Link, J. S., Kaplan, I. C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., *et al.* 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries, 12: 171–188.

Gell, F. R., and Roberts, C. M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends in Ecology & Evolution, 18: 448–455.

Gerber, L. R., Botsford, L. W., Hastings, A., Possingham, H. P., Gaines, S. D., Palumbi, S. R., and Andelman, S. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications, 13: 47–64.

Graham, N., Ferro, R. S. T., Karp, W. A., and MacMullen, P. 2007. Fishing practice, gear design, and the ecosystem approach—three case studies demonstrating the effect of management strategy on gear selectivity and discards. ICES Journal of Marine Science, 64: 744–750.

Hall, M. A., Alverson, D. L., and Metuzals, K. I. 2000. By-catch: problems and solutions. Marine Pollution Bulletin, 41: 204–219.

Hamel, O. S., Sethi, S. A., and Wadsworth, T. F. 2009. Status and future prospects for lingcod in waters off Washington, Oregon, and California as assessed in 2009. Pacific Fishery Management Council, Portland, OR.

Hasselman, B. 2015. nleqslv: solve systems of non linear equations. R package version 2.9.

Hastings, A., and Botsford, L. W. 2003. Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications, 13: 65–70.

Hixon, M. A., Johnson, D. W., and Sogard, S. M. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science, 71: 2171–2185.

Kaplan, I. C., Marshall, K. N., Hodgson, E., and Koehn, L. 2014. Update for 2014 methodology review: ongoing revisions to the spatially explicit Atlantis Ecosystem Model of the California Current. NOAA Fisheries, Northwest Fisheries Science Center, Seattle, WA.

Lauck, T., Clark, C. W., Mangel, M., and Munro, G. R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications, 8: S72–S78.

Law, R. 2007. Fisheries-induced evolution: present status and future directions. Marine Ecology Progress Series, 335: 271–277.

Lessard, R. B., Martell, S. J., Walters, C. J., Essington, T. E., and Kitchell, J. F. 2005. Should ecosystem management involve active control of species abundances. Ecology and Society, 10: 1.

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., Airamé, S., et al. 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series, 384: 33–46.

Levin, P. S., Fogarty, M. J., Murawski, S. A., and Fluharty, D. 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. PLoS Biology, 7: e1000014.

Link, J. S. 2004. Using fish stomachs as samplers of the benthos: integrating long-term and broad scales. Marine Ecology Progress Series, 269: 265–275.

Link, J. S., and Garrison, L. P. 2002. Trophic ecology of Atlantic cod Gadus morhua on the northeast US continental shelf. Marine Ecology Progress Series, 227: 109–123.

Lomeli, M. J. M., and Wakefield, W. W. 2012. Efforts to reduce Chinook salmon (Oncorhynchus tshawytscha) and rockfish (Sebastes spp.) bycatch in the U.S. west coast Pacific hake (Merluccius productus) fishery. Fisheries Research, 119–120: 128–132.

Love, M. S., Yoklavich, M., and Thorsteinson, L. K. 2002. The Rockfishes of the Northeast Pacific. University of California Press, Oakland, CA.

Mangel, M., and Levin, P. S. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 360: 95–105.

Marshall, K. N., Stier, A. C., Samhouri, J. F., Kelly, R. P., and Ward, E. J. 2016. Conservation challenges of predator recovery. Conservation Letters, 9: 70–78.

O'Keefe, C. E., and DeCelles, G. R. 2013. Forming a partnership to avoid bycatch. Fisheries, 38: 434–444.

Parker, S. J., McElderry, H. I., Rankin, P. S., and Hannah, R. W. 2006. Buoyancy regulation and barotrauma in two species of nearshore rockfish. Transactions of the American Fisheries Society, 135: 1213–1223.

Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, ecosim, and ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science, 57: 697–706.

PFMC (Pacific Fishery Management Council). 2014. Status of the Pacific Coast Groundfish Fishery: Stock Assessment and Fishery Evaluation. Pacific Fishery Management Council, Portland, OR.

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., et al. 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish and Fisheries, 15: 43–64.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., et al. 2004. Ecosystem-based fishery management. Science, 305: 346–347.

Plagányi, É. E., Punt, A. E., Hillary, R., Morello, E. B., Thébaud, O., Hutton, T., Pillans, R. D., et al. 2014. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish and Fisheries, 15: 1–22.

Punt, A. E., and Butterworth, D. S. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals Arctocephalus pusillus pusillus and the Cape hakes Merluccius capensis and M. paradoxus. South African Journal of Marine Science, 16: 255–285.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, J. C., and Tapper, S. C. 1996. Control of mammalian predators in game management and conservation. Mammal Review, 26: 127–155.

Scharf, F. S., Juanes, F., and Rountree, R. A. 2000. Predator size – prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series, 208: 229–248.

Simberloff, D. S. 1974. Equilibrium theory of island biogeography and ecology. Annual Review of Ecology and Systematics, 5: 161–182.

Smith, A. D. M., Sainsbury, K. J., and Stevens, R. A. 1999. Implementing effective fisheries-management systems–management strategy evaluation and the Australian partnership approach. ICES Journal of Marine Science, 56: 967–979.

Somers, K. A., Bellman, M., Jannot, J., Riley, N., and McVeigh, J. 2014. Estimated discard and catch of groundfish species in the 2013 U.S. West Coast fisheries. NOAA Fisheries, NWFSC Observer Program, Seattle, WA.

Szoboszlai, A. I., Thayer, J. A., Wood, S. A., Sydeman, W. J., and Koehn, L. E. 2015. Forage species in predator diets: synthesis of data from the California Current. Ecological Informatics, 29: 45–56.

Taylor, I. G., and Wetzel, C. 2011. Status of the U.S. yelloweye rockfish resource in 2011. Pacific Fishery Management Council, Portland, OR.

Tissot, B. N., Hixon, M. A., and Stein, D. L. 2007. Habitat-based submersible assessment of macro-invertebrate and groundfish assemblages at Heceta Bank, Oregon, from 1988 to 1990. Journal of Experimental Marine Biology and Ecology, 352: 50–64.

Van Kirk, K. F., Quinn, T. J., Collie, J. S., and A'Mar, Z. T. 2015. Assessing uncertainty in a multispecies age-structured assessment framework: the effects of data limitations and model assumptions. Natural Resource Modeling, 28: 184–205.

Walters, C. 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? Bulletin of Marine Science, 66: 745–757.

White, J. W., Botsford, L. W., Hastings, A., Baskett, M. L., Kaplan, D. M., and Barnett, L. A. K. 2013. Transient responses of fished populations to marine reserve establishment. Conservation Letters, 6: 180–191.

Williams, S. 2014. Report on the predation index, predator control fisheries, and program evaluation for the Columbia River Basin experimental northern pikeminnow management program. 2014 Annual Report. Pacific States Marine Fisheries Commission.

Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? Trends in Ecology & Evolution, 16: 78–84.

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