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INAUGURAL ARTICLE

Marine reserves solve an important bycatch problem in fisheries

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Management of the diverse fisheries of the world has had mixed success. While managing single species in data-rich environments has been largely effective, perhaps the greatest challenge facing fishery managers is how to deal with mixed stocks of fish with a range of life histories that reside in the same location. Because many fishing gears are nonselective, and the costs of making gear selective can be high, a particular problem is bycatch of weak stocks. This problem is most severe when the weak stock is long-lived and has low fecundity and thus requires a very long recovery time once overfished. We investigate the role that marine reserves might play in solving this challenging and ubiquitous problem in ecosystem-based management. Evidence for marine reserves' potential to manage fisheries in an ecosystem context has been mixed, so we develop a heuristic strategic mathematical model to obtain general conclusions about the merits of managing multispecies fisheries by using reserves relative to managing them with nonspatial approaches. We show that for many fisheries, yields of strong stocks can be increased, and persistence of weak stocks can be ensured, by using marine reserves rather than by using traditional nonspatial approaches alone. Thus, reserves have a distinct advantage as a management tool in many of the most critical multispecies settings. We also show how the West Coast groundfish fishery of the United States meets these conditions, suggesting that management by reserves may be a superior option in that case.

fishery management | marine protected area | weak stocks | bycatch

Fisheries management has a mixed record of success in the sea (1–3). Despite many successes (4, 5), failures are common and reflect limitations of science, policy, and management. Arguably, the biggest scientific failure is the continued reliance on single-species models in situations, when more ecosystem-based approaches are warranted (1, 2, 6). Although management decisions are often based on one target species, most fisheries simultaneously impact the dynamics of other secondary targets, or bycatch. If sustainable catch rates differ across these species, optimal decisions for one species may have disastrous effects for others; these are "weak stocks" that are driven to unsustainably low levels when fishing is optimized for the target species. Although this problem has been well known for 50 y or more (7), it remains one of the most pressing challenges in fisheries, and weak stock disasters are becoming more commonplace (8). The traditional approach for dealing with this problem is to reduce the catch rates of all species to ensure persistence of the weak stock; this often entails severe cutbacks in the harvest of target species. Examples include nearly all groundfish fisheries on the west and east coasts of North America (8).

Given the nature of the problem, an approach based on strategic rather than detailed models is an important step. We specifically model a situation where there is a target species that is the focus of economic activity and there is a second species, the weak stock, that is harvested as bycatch and is in danger of extirpation. We take as given that the fishery manager wants to maximize catch of the strong stock while ensuring persistence of the weak stock. The traditional approach for doing so requires reducing catch rates of all species; this often involves unacceptably high costs (8). While we focus on strong stock yield, in some cases, there may also be small economic benefits from the weak stock. In those cases, our strategic approach will also provide general guidance. Here, we show, using simple multispecies models, that a surprisingly effective solution may lie in the use of fisheries management incorporating marine reserves. If the weak stock is longer-lived and matures later than the target species, management by marine reserves always produces a higher sustainable yield, and higher stock abundance, than could be achieved by single-species approaches without a marine reserve.

Marine reserves are areas of the ocean closed to fishing. Historically, such marine-protected areas were created primarily to achieve conservation goals. By reducing fishing mortality and habitat damage, population densities and average size of previously fished species commonly increase significantly (9–11). Moreover, since the boundaries of marine reserves do not constrain the movement of adults or the microscopic larvae they release to the plankton, some of the benefits from protection are exported beyond reserve borders. As a result, the potential spillover of benefits to fished habitats has focused increasing attention on the fisheries impacts of closures (12–18). Although the integration of marine reserves into fisheries models is still relatively immature, theoretical studies suggest that management including reserves can often do as well as (12, 13, 15) or better than (12, 19) nonspatial forms of management, although empirical evidence is more mixed (14, 20). Since marine reserves simultaneously impact many species in an area, they are increasingly touted as an important component of ecosystem-based management efforts. Initial models of marine reserves focused on single species or did not include dynamics (12, 15), even though

Significance

Bycatch, where one species is unintentionally caught in pursuit of another species, is one of the most ubiquitous and crippling challenges in global fisheries. The usual solution is to dramatically reduce take of the target species to allow "weak stock" persistence. Using a general strategic model, we show that establishing areas closed to fishing can alleviate, or even completely eliminate, this problem. If the weak stock is long-lived, but slow to reproduce, significantly higher yields can be obtained by using reserves than by using fishing effort controls alone. We emphasize that this is the problem plaguing the US West Coast groundfish fishery, suggesting that in that fishery, marine reserves may be a solution that simultaneously benefits fishermen and conservation.

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the problem has long been recognized (7). Others have also considered issues of multiple species and the role of reserves (19, 21, 22), but have not specifically addressed the important question we focus on here. In particular, advances based on simulation approaches (23, 24) have yielded important insights into particular fisheries. We take a different approach to developing principles for multispecies management by using simple, heuristic models to examine whether marine reserves could help resolve aspects of the weak-stock fisheries problem.

Our scientific understanding of the complex dynamics of multispecies fisheries is still limited (25). Simple models with clearly stated assumptions can provide general principles to guide decisions and can point to future directions for more detailed studies. In the context of management of fisheries through the use of marine-protected areas, one example of such a model was developed by Hastings and Botsford (15), who showed conditions under which maximum sustainable yield from effort control would be exactly the same as maximum sustainable yield obtained from setting aside a portion of the habitat as a marine reserve. Although that model was stylized, so the specific assumptions of the model may never be exactly met in practice, both the generality of the conclusions and the ease with which the dependence of the conclusions on the assumptions can be evaluated were key advantages. In fact, the impact of changing assumptions could be deduced in many cases without formal calculations. We build on that model here.

We make a number of simplifying and conservative assumptions to get a basic understanding of the problem, recognizing that, in any particular fishery, not all of the assumptions may be met and that more detailed models will be needed to develop more detailed management plans. Our arguments build on earlier models for single species (12, 15), but with appropriate extensions to deal with a multispecies fishery. In particular, we assume that adults are sufficiently stationary to remain within the reserve; that larvae are so widely distributed that we can ignore their spatial arrangement; that issues arising from explicit consideration of age structure can be ignored; and that all density dependence occurs at the time of larval settlement. The effects of deviations from these assumptions can at first be dealt with by verbal arguments, and then, in future work, by more detailed models. We further assume that the only interaction between species is that they are subject to the same fisheries management—the same harvest rate outside reserves and the same protection afforded by a set of reserves. Other interactions are not specifically considered. As a way to demonstrate the robustness of our conclusions, we will comment on how relaxing these assumptions will affect key model results.

We proceed in several ways using our simple model. We first use an analytic approach to demonstrate the potential for reserves to give rise to higher yield of a strong stock, and higher population levels of the weak stock, than would management without a reserve. This will indicate the kinds of life histories for weak and strong stocks where reserves would be advantageous. We then illustrate these results and extend them to conditions that cannot be investigated analytically for general parameter values using a numerical investigation of our model. Our analytic approach begins with conditions for persistence of the weak stock. However, this approach could include persistence at unacceptably low levels, perhaps implying persistence only in a deterministic model and not in a field situation. We thus complement the analytic demonstration of the underlying principle with more detailed numerical approaches, parameterized with values from the West Coast groundfish multispecies system. Instead of focusing on the persistence boundary for the weak stock, we require the weak stock to be above a threshold level.

Even though our approach is a strategic one, we finish by making an empirical comparison with parameters representative of weak and strong stocks for the US West Coast groundfish fishery. This highly diverse fishery highlights the potential practical importance of our findings, even though it necessarily simplifies the life history details and other aspects of this fishery.

Model and Analysis

We start with a simple, single-species model with and without reserves. The dynamics of multiple species in a reserve network can then be described by keeping track of the densities of each species inside and outside of reserves. In the absence of a reserve, the discrete-time population dynamics for species i are given by:

$$n_{i,t+1} = E_i\left[f_i(m_i n_{i,t}) + a_i n_{i,t}\right] \quad \textbf{[1]}$$

where $n_{i,t}$ is the density (biomass per length of coastline, where the coastline is normalized to a length of one) of species i at time t, E_i is the escapement, the fraction of the stock that is left unharvested, the function $f_i(\cdot)$ describes the survival of young until they recruit to the adult population, m_i is the per capita fecundity, and a_i is the survivorship of adults. So far, this model is identical to ref. 15. We denote by c the fraction of the coastline in a no-take marine reserve network. We will keep track of fish stocks in two locations [inside the reserve (R) and outside the reserve (O)], so n_{it}^R is the density of species i inside the reserve and $n_{i,t}^O$ is the density outside the reserve in period t.

Several specific assumptions should be emphasized so that we later can discuss implications of relaxing these assumptions. We do not include explicit space; we are assuming that larvae are widely and uniformly distributed. We do not include specific aspects of age structure. We ignore economic aspects such as the cost of harvest as a function of fish density. In what follows, we only focus on steady-state yields from the strong stock and do not explicitly include issues related to yield from the weak stock.

We focus on two species, with subscripts $i = w$ for the weak stock and $i = s$ for the "strong" stock. Here, the strong stock is the primary target of the fishery. The weak stock is one that would be reduced to an unacceptably low level (including extinction) with continued harvest of the strong stock at a rate that maximizes strong-stock yield in the absence of reserves. We formalize this definition below. We assume that these species are biologically independent, but that harvesting is indiscriminate in the sense that the harvest makes the escapement the same for both species, $E_w = E_s = E$, and, similarly, reserves provide full protection for both species. This symmetry implies that the two policy levers available to fishery managers are c (fraction of coastline in reserve) and E (fraction of stock outside reserves that is left unharvested). We will use an equilibrium analysis, so we focus on steady state. For convenience, we use escapement as the fishery management instrument, but it is a straightforward matter to derive the commensurate harvest quotas. Obviously, questions about dealing with uncertainties and a fishery that is currently either overexploited or underexploited would be an important next step in applying this model to real-world settings.

Incorporating all of this information, we can immediately write down a system of equations that describes, in steady state so the subscript t is not used, the densities of species i in and out of reserves, as follows:

$$n_i^R = f_i(m_i(cn_i^R + (1-c)n_i^O)) + a_i n_i^R \quad \textbf{[2]}$$

$$n_i^O = E\left[f_i(m_i(cn_i^R + (1-c)n_i^O)) + a_i n_i^O\right] \quad \textbf{[3]}$$

And steady-state yield is given by:

$$Y_i = (1-E)(1-c)f(m_i cn_i^R + (1-c)n_i^O) + a_i n_i^O \quad \textbf{[4]}$$

We assume that the objective of fishery management is to maximize equilibrium yield of the strong stock, but that the weak stock must not be driven extinct. Eqs. **2–4** can be analyzed to select a policy that achieves this goal; we make use of two important benchmarks. First, define by E_s^* the escapement that maximizes the yield described by Eq. **4** when $c = 0$—that is, it is the optimal escapement for the strong stock in the absence of reserves. Second, define by c_s^* the reserve size that maximizes Eq. **4** when $E=0$—that is, it is the optimal reserve size for the strong stock if everything outside the reserve is harvested. Ref. 15 showed that the strong stock yield arising from E_s^* is equivalent to the strong stock yield arising from c_s^*; we denote this yield by Y_s^*. Mathematically, we define a weak stock as a species that goes extinct under the escapement rate ($E=E_s^*$). In other words, if we manage the fishery with traditional means (without a reserve) and choose effort to maximize yield of the strong stock, the weak stock will go extinct.

Without a reserve, ensuring persistence of a weak stock necessarily requires increasing the escapement of the strong stock beyond what would produce maximal yield (i.e., setting $E>E_s^*$). This escapement generates a loss of yield for the strong stock (so $Y_s<Y_s^*$). We take as a starting point the observation (15) that management of any single stock could achieve equivalent yield with either an optimal escapement policy (with no reserve) or with a reserve-only policy (with no escapement outside the reserve). By using this insight, our analysis first asks whether conditions exist under which the reserve-only policy (where $c=c_s^*$ and $E=0$) leads to persistence of the weak stock. If such conditions exist, the reserve policy will both ensure the persistence of the weak stock and ensure maximal profit for the strong stock. We begin by determining a general condition for the persistence of the weak stock and then determine conditions where, under the reserve-only policy that produces optimal yield from the strong stock, the weak stock persists. This will indicate the kinds of life histories where reserves will be advantaged by this approach.

It is also possible that single-species-optimal yield from the strong stock is never possible, but that managing with a reserve still ensures persistence and produces a higher yield than does managing without a reserve. In that case, management that maintains the weak stock is either through a combination of reserves and escapement (escapement outside reserves is positive), or escapement outside reserves is zero, but the fraction of the coastline in reserves is greater than would produce the highest yield from the strong stock. As algebraic conditions in this case become frightfully complex, we present numerical results only.

We begin the analysis by determining conditions for the persistence of the weak stock, where we will make the additional assumption that the per capita survival of young until they recruit is a monotone decreasing function of settling juveniles. This will provide an algebraic condition describing a weak stock—namely, that it does not persist when the escapement is set to maximize sustainable yield of the strong stock.

Starting with the dynamic model implied by Eqs. **3** and **4**, we derive the conditions under which the equilibrium with the weak stock at 0 is unstable (and, thus, the weak stock is persistent). The persistence of the weak stock requires that at least one eigenvalue of the Jacobian is positive:

$$J=\begin{bmatrix} f'(0)mc+a-1 & f'(0)m(1-c) \\ Ef'(0)mc & E\left[f'(0)m(1-c)+a\right]-1 \end{bmatrix} \quad \textbf{[5]}$$

Using ideas from Perrron–Frobenious theory, one sees that the persistence boundary for a species is given by the condition that the determinant of this matrix be zero. Consequently, the persistence boundary for the weak stock is given by

$$E_w(c)=\frac{a_w+cf_w'(0)m_w-1}{a_w^2+a_w(f_w'(0)m_w-1)-f_w'(0)m_w+cf_w'(0)m_w} \quad \textbf{[6]}$$

For any reserve size c, if escapement $E<E_w(c)$, then the weak stock dies off, and if $E>E_w(c)$, then the weak stock persists. In the absence of a reserve (so $c=0$), this becomes:

$$E_w(0)=\frac{a_w-1}{a_w^2+a_w(f_w'(0)m_w-1)-f_w'(0)m_w} \quad \textbf{[7]}$$

which reduces to

$$E_w(0)=\frac{1}{a_w+f_w'(0)m_w} \quad \textbf{[8]}$$

Thus, by our definition of a weak stock, $E_s^*<E_w(0)$, so the following condition must hold for a weak stock:

$$E_s^*<\frac{1}{a_w+f_w'(0)m_w} \quad \textbf{[9]}$$

We now turn to the reserve-only policy and ask if the weak stock will persist if we institute a policy of management only by reserves with no escapement outside reserves, so $c=c_s^*$ and $E=0$ outside the reserve. The reserve size can be denoted:

$$c_s^*=E_s^*-(1-E_s^*)\frac{a_sn_s^*}{f_s(m_sn_s^*)} \quad \textbf{[10]}$$

where n_s^* is the population level of the strong stock at the optimal harvest level.

If the persistence condition for the weak stock is satisfied when $E=0$ and reserves are at the level c_s^*, then clearly the reserve policy provides higher yield than the no-reserve policy. From Eq. **6**, when the escapement rate is zero, the persistence condition for the weak stock becomes

$$0<f_w'(0)m_wc+a_w-1 \quad \textbf{[11]}$$

Denoting this threshold reserve size for the weak stock by c_w and rearranging gives:

$$c_w=\frac{1-a_w}{f_w'(0)m_w} \quad \textbf{[12]}$$

Even if all fish are harvested outside the reserve, if $c>c_w$, then the weak stock persists; if $c<c_w$, then it dies off. So, a necessary and sufficient condition for the weak stock to persist under a reserve-only strong stock policy is:

$$c_s^*>\frac{1-a_w}{f_w'(0)m_w} \quad \textbf{[13]}$$

If Eqs. **9** and **13** hold, then we are ensured that (*i*) the weak stock will, in fact, die off under traditional (no-reserve) management for the strong stock; and (*ii*) the weak stock will persist under reserve-only management for the strong stock. Because strong stock yield is identical in the two cases, Eqs. **9** and **13** are sufficient to prove that reserves offer a yield advantage to the strong stock fishery, while ensuring the persistence of the weak stock.

A simple numerical example shows that this is typically the case when the strong stock has a low value of survival. For example, if E^* is 0.3, which is a typical value (15), and the survival of the strong stock is taken to be very small ($a_s\ll 1$), then the condition under which the weak stock goes extinct under traditional harvest and survive with management solely by reserves becomes

$$\frac{1-a_w}{f_w'(0)m_w}<0.3<\frac{1}{a_w+f_w'(0)m_w} \quad \textbf{[14]}$$

which is satisfied, for example, when $a_w=0.8$ and $0.67<f_w'(0)m_w<2.5$.

Clearly, as the adult survivorship of the strong stock increases, if a_s is greater than zero, the conditions for weak-stock persistence are more stringent. We now move to the more general case where full yield for the strong stock may not be possible; we investigate this numerically.

Numerical Approach

Although the analytic results provide a clear demonstration of the potential advantages of marine reserves for reducing the negative impacts of bycatch, there are many aspects of our model that are not amenable to analytic analyses. Given the relative simplicity of the model, it is possible to investigate a range of conditions numerically. We do this both for general values and for parameters estimated from the West Coast groundfish fishery.

To implement this model numerically, we need fecundity and survivorship parameters (m, a) and a specific function for recruitment that includes postdispersal density dependence and survival, $f(\cdot)$ for both the strong and weak stock. For $f(\cdot)$, we use the Beverton–Holt functional form:

$$f(n) = \frac{\alpha n}{1 + n/\beta} \quad \textbf{[15]}$$

where α is the initial slope (at zero). Under this specification for $f(n)$, we can calculate the unfished equilibrium (i.e., the carrying capacity):

$$n_{\text{unfished}} = \frac{\beta}{m}\left(\frac{\alpha m}{1-a} - 1\right) \quad \textbf{[16]}$$

So the persistence requirement (in an unfished state) is:

$$\frac{\alpha m}{1-a} > 1 \quad \textbf{[17]}$$

Numerical Results

Our main results are illustrated by Fig. 1. The figure shows the yield of the strong stock and the persistence of the weak stock, for a range of reserve (c) and escapement (E) policies for three classes of weak stock species. The background shading is proportional to equilibrium strong stock yield, where lighter shading indicates higher yield. The solid curve represents the persistence boundary for the weak stock (here we assume this occurs at 5% of carrying capacity); left and below the curve the weak stock dies off, and right and above the curve it persists. Circles indicate escapement policies that maximize strong stock yield for any given reserve size; circle size indicates strong stock yield; and circle color indicates weak stock abundance.

The three examples of weak-stock species represented in Fig. 1 pose different challenges. One driver could be the scope of differences in the life history parameters of the weak vs. strong stock species. In the first case (Fig. 1*A*), maximizing strong-stock yield in the absence of a reserve will clearly cause the weak stock to die off (the largest no-reserve circle is well inside the persistence boundary). Simply increasing escapement without a reserve (moving up the 0% reserve axis) entails an unavoidable loss in strong-stock yield, but can eventually guarantee weak-stock persistence. Alternatively, moderately sized reserves (between $c = 25$ and 40%), with the appropriate choice of escapement outside the reserve, can both ensure persistence of the weak stock (circles to the right of the persistence boundary) and produce yields equivalent to what would have been possible under optimal single-species management (circles are the same size as the left-most circle). While even larger reserves will ensure persistence of the weak stock, they also entail a loss in yield of the strong stock (as c increases above 40%, circles diminish in size). Under these parameter values, any reserve between 25 and 40%, matched with appropriate escapement, can achieve maximum sustainable yield of the strong stock and ensure persistence of the weak stock. This illustrates our main finding.

The second case (Fig. 1*B*) illustrates a weak stock species that requires more aggressive actions to achieve persistence. Here, the persistence boundary is to the right of all possible combinations of reserve size and escapement that can maintain maximum sustainable yield for the strong stock. As a result, all options with persistence of the weak stock necessarily require a yield compromise for the strong stock. The magnitude of the compromise differs, however, between the reserve and escapement-only options. In this case, the yield with a very large reserve is much larger than the best option with sufficiently low escapement for persistence.

Finally, in Fig. 1*C*, the weak stock is persistent with maximum strong-stock yield, even with no marine reserve. The persistence boundary is to the left of the entire curve of options that maximize strong-stock yield. Although this case does not require a marine reserve, increases in reserve size up to 40% continue to grow the weak-stock population with no compromise to the strong-stock yield. As the reserve size increases to 40%, the weak-stock population grows from $\sim$5% of its unfished population size to 23%.

To help ground the three generic cases illustrated in Fig. 1, we also looked at model predictions using data for a group of weak and strong stocks from the highly diverse Eastern Pacific groundfish fishery, which has historically been plagued by closures due to overfished weak stocks (Fig. 2). Given the very large number of stocks in this fishery (>90 species), we focus on a few illustrative cases. We show projections for four important overfished stocks—bocaccio, darkblotched rockfish, Pacific Ocean perch, and yelloweye rockfish. For each case, the comparative strong stock is Dover sole (*Microstomus pacificus*), a stock that is currently viewed as healthy with large annual landings (26). For the prior examples, we used a persistence curve defining characteristics that would lead to a population at 5% of its historical unfished size—perhaps enough to forestall extinction, but a very small population size. In this example, we also show the 20 and 40% persistence boundaries for each weak stock. The latter is meant to parallel the current US policy of rebuilding weak stocks back to levels closer to where their own fishery yields would be maximized. Results are similar across the four weak-stock species; here, we discuss two key findings. First, all four weak-stock species can be made persistent at the 5% level with no compromise in strong-stock yield, but only if marine reserves are used (these reserves would be on the order of 10% of the area). Second, to achieve higher levels of weak-stock abundance (say, 20 or 40% of carrying capacity) will require some unavoidable compromises in strong-stock yield, but this compromise is generally less stringent when reserves are used. For example, yelloweye rockfish (Fig. 2*D*) can achieve 20% of its carrying capacity either with no reserve (but a loss of 32% in yield of petrale sole) or with a 21% reserve (foregoing just 9% in yield of petrale sole). The only case we found in which the no-reserve policy might be preferred is with bocaccio (which, by these calculations, is not a true weak stock, because it could sustain a population of $\sim$5% of carrying capacity even under effort-only maximum sustainable yield management of the strong stock). Even in that case, the losses are very small. For example, for bocaccio to achieve 20% persistence, the no-reserve policy entailed a strong-stock yield cost of 7%, while the reserve policy entailed a strong-stock yield cost of 10%.

Discussion

The problem of weak stocks, and bycatch more generally, is one of the most important challenges facing fisheries management today (27, 28). Without selective gear or practices that can greatly reduce the catch rates of weak stocks, traditional fisheries management has a limited arsenal to combat the problem. The most widespread policy approach to this problem has been to reduce harvest rates of all species to avoid extinction of the weak stocks. However, the costs of this approach in yield of the strong stock can be substantial. It is intuitive that the problem is most severe when the weak stock is much longer-lived (high survivorship), late maturing, and has lower fecundity than the target stock. However, we have shown that these are the precise conditions under which reserves provide the greatest benefit. A long-lived, slow-reproducing weak stock is also the case where overfishing can have the longest-lasting impact, since its recovery following management failure may be exceedingly slow.

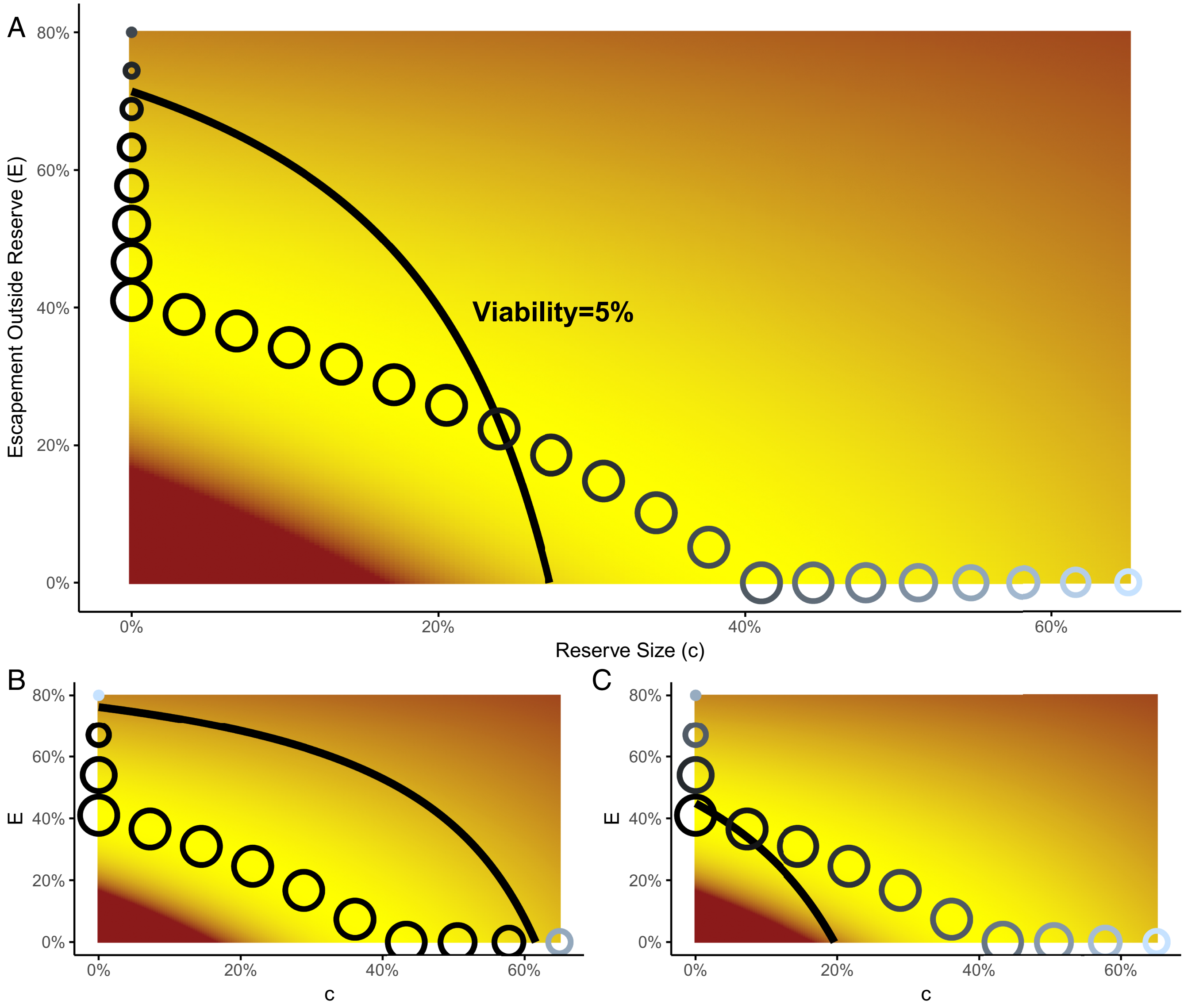

Fig. 1. Strong stock yield (background color and circle size) and weak stock persistence boundary (bold curve, representing 5% of weak-stock carrying capacity) for combinations of reserve size (*c*) and strong-stock escapement outside the reserve (*E*) for three hypothetical species pairs. The persistence boundary of 5% is arbitrary; similar results would be obtained for other small population levels, including the level of 0 used in the analytic calculations. The strong stock yield (circle size) should be compared with the largest circles to get an appreciation of the yield for that choice of reserve size and escapement as compared with the maximum yield. Only parameter combinations above and to the right of the bold line allow persistence of the weak stock; circle shading indicates equilibrium weak stock population size. Shown are three different hypothetical weak stock species for which any reserve between 25 and 40% will increase strong stock yield and ensure weak stock persistence (*A*); ensuring persistence of the weak stock requires either a very large reserve (60%) or a very high escapement (75%), although the reserve option produces much better strong stock yield (*B*); and even without a reserve, the weak stock is persistent and the strong stock yield is maximized, although the weak stock would benefit from a reserve of up to 40% without any compromise in strong stock yield (*C*).

We have shown that for any multispecies fishery with weak stock limitations where the weak stock is longer-lived and less fecund than the target species, the yield from management with reserves will always be higher than the yield from traditional management. While this general conclusion is independent of the functional form of density dependence (provided it meets the conditions stated above), the functional form of density dependence will determine the optimal harvest rates or optimal reserve sizes for the target species, which, in turn, determines when the weak stock is at risk.

A heuristic understanding of our results begins by noting that reserves are more of a benefit for species with high natural adult survivorship than they are for species with low adult survivorship. All life histories involve trade-offs, so species with high adult survivorship typically have low fecundity, both generally (29) and in the West Coast groundfish system (26). Species with low fecundity are the ones most at risk from overfishing, and hence are weak stocks. However, since species with low fecundity typically have high survivorship, reserves will be a benefit to these weak stocks.

Obviously, there are both other potential solutions to the problem of bycatch and additional ways that the assumptions of our model would be violated. It might seem that more selective gear or other approaches could have advantages when used to reduce bycatch, but these efforts would also have potentially significant costs from less-efficient catches of the target species (27, 28). Conversely, our model does not assign higher costs to catch

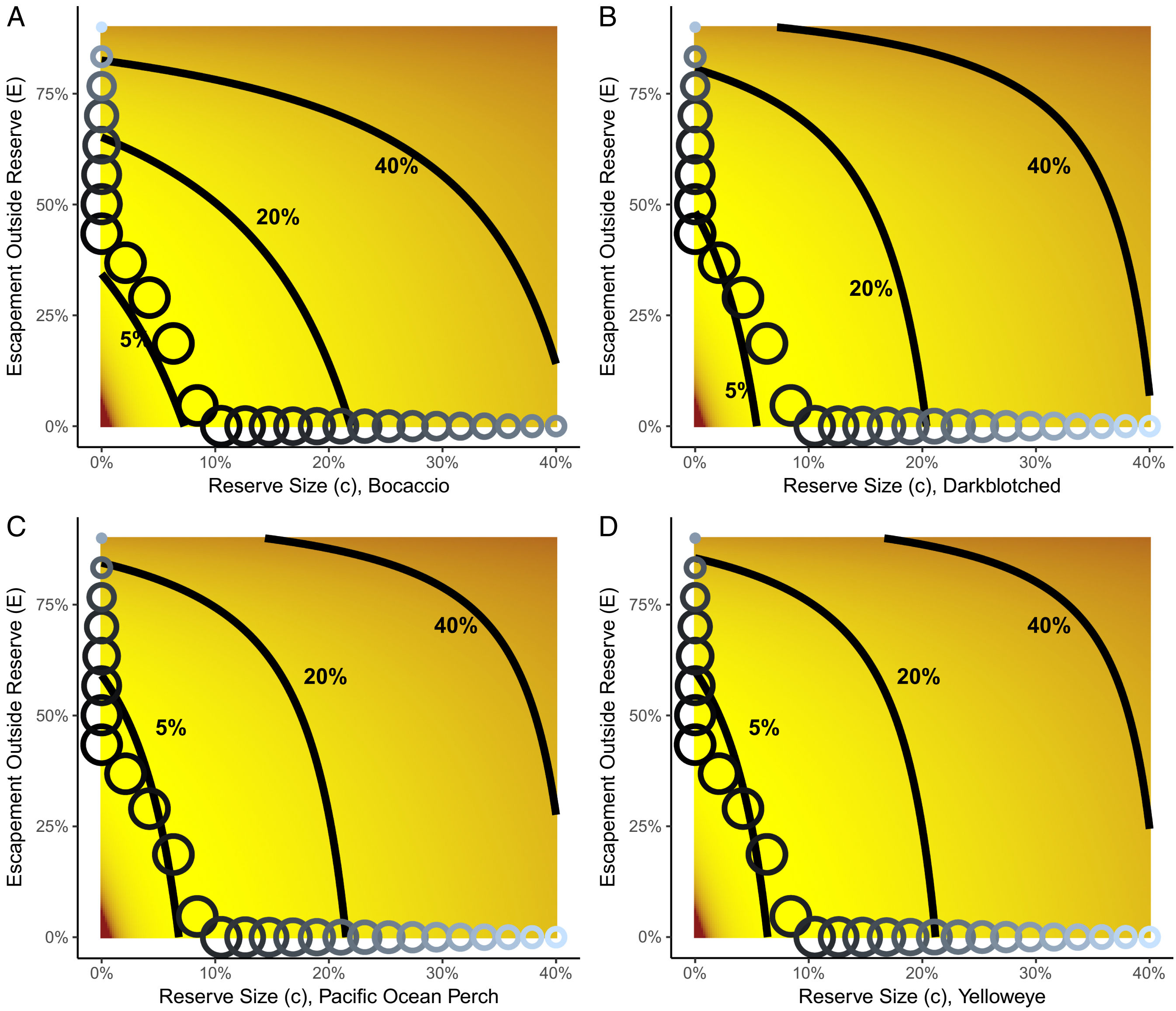

Fig. 2. Strong-stock yield (background color and circle size) and weak-stock persistence boundary (bold curves, representing 5, 20, or 40% of weak-stock carrying capacity) for combinations of reserve size (c) and strong-stock escapement outside the reserve (E) for the West Coast groundfish fishery, with Dover sole as the strong stock and four different weak stocks. Parameters are determined as described in *Materials and Methods*, based on the recent stock-assessment summary (26). See Fig. 1 for further description. Each panel has a different weak stock: bocaccio (*A*), darkblotched (*B*), Pacific Ocean perch (*C*), and yelloweye (*D*), with the same strong stock.

at lower stock levels outside reserves as compared with stock levels that would exist if management were solely limiting effort without reserves. These two observations suggest that strategies with some escapement outside reserves could turn out to be the most economically beneficial. A full consideration of this problem would require a model and approach that was far more detailed and specific and that would consequently have less general applicability.

Table 1. Parameters used in Fig. 1 (hypothetical) and Fig. 2 (West Coast fisheries)

Parameter	Fig. 1*A*	Fig. 1*B*	Fig. 1*C*	Fig. 2*A*	Fig. 2*B*	Fig. 2*C*	Fig. 2*D*
a_w	0.85	0.5	0.7	0.85	0.939	0.95	0.955
m_w	1.6	1.4	2.5	1	1	1	1
α_w	0.4	0.6	0.78	6.26	13.62	2.67	3.14
β_w	5	5	5	825.8	204.05	3495.3	72.59
a_s	0.01	0.01	0.01	0.87	0.87	0.87	0.87
m_s	8.5	8.5	8.5	1	1	1	1
α_s	0.7	0.7	0.7	16	16	16	16
β_s	20	20	20	23799	23799	23799	23799

The groundfish fishery off the West Coast of the United States illustrates the importance of our results (Fig. 2). In this case, the weak (overfished) stocks are all among the longest-lived (highest survivorship), and the gear was typically not very selective (8). Thus, the general import of our model strongly suggests that reserves may be a superior management tool for this system in particular, and this kind of system in general. We should point out, however, that the multispecies catch share has led to great advances in selectivity motivated by economic incentives (24, 30). Somewhat ironically, that fishery has actually already established significant closures for rockfish conservation. However, these closures were not designed as part of the fishery management system, nor are they appropriately monitored to determine the extent to which they contribute to weak stock persistence. Indeed, given their size ($\sim$50% of the fishable area is off-limits to trawl fishing), it is quite possible that they are sufficiently large to guarantee not only persistence of weak stocks, but high populations of weak stocks (of 40–50% of carrying capacity).

We have shown that spatial management using permanent marine reserves can produce higher yields in these challenging weak-stock situations. More importantly, though, we have shown that, for a wide range of life history combinations, maximum yields are not compromised by spatial closures that guarantee the persistence of weak stocks. Even when yields are constrained in the marine reserve case, the yield exceeds those achievable by nonspatial management. Thus, although there is debate in the single species case about the merits of spatial vs. nonspatial management, in the more realistic multispecies setting, reserves can be a broadly superior management strategy. Moreover, these benefits of management by reserves are likely conservative, since we have ignored three real-world characteristics that should further enhance the benefits of spatial management using marine reserves, including: (*i*) population age structure, which allows reserves to accumulate older, more fecund adults; (*ii*) limited larval dispersal, which allows marine reserves to help weak stocks persist with even smaller closures, since a greater fraction of young recruit back to the protection of reserves; and (*iii*) legal mandates that focus on maintaining weak stocks at some percentage of unfished population density, rather than the less restriction persistence criterion we have used. Of course, none of these benefits of marine reserves accrue unless adults are sedentary enough to receive protection within the bounds of the reserves. Since the fraction of habitat needed in marine reserves to guarantee weak stock persistence is relatively large, this movement constraint may only be a challenge for the most pelagic species. Overall, we find that management of fisheries by using well-designed marine reserves, combined with sensible target fishery management outside, may provide broad economic and ecological benefits in multispecies contexts.

Materials and Methods

We used data from the recent stock-assessment summary (26) to derive the parameters used in Fig. 2. The report lists male and female mortality. If they differ, we use the average. From the values for R_0 and steepness h given in this report, we can calculate the parameters in our form of the Beverton–Holt model using standard formulae, such as those given in ref. 31. Thus, up to a scaling factor that does not change our results, the parameters in Eq. **15** can be calculated as

$$\alpha = 4h/(1-h) \qquad [18]$$

and

$$\beta = \frac{R_0 * (1-h)}{5h-1} \qquad [19]$$

We recognize that there are potential statistical issues (32) involved in the estimation and use of these parameters, but these issues will not affect the general nature of our conclusions. To run any given simulation requires a total of eight parameters (four representing the weak stock, subscripted by w, and four representing the strong stock, subscripted by s). Table 1 summarizes these eight parameters for each of the seven subplots in Figs. 1 and 2.

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