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BRIEF COMMUNICATION

Ocean zoning within a sparing versus sharing framework

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Abstract

The land-sparing versus land-sharing debate centers around how different intensities of habitat use can be coordinated to satisfy competing demands for biodiversity persistence and food production in agricultural landscapes. We apply the broad concepts from this debate to the sea and propose it as a framework to inform marine zoning based on three possible management strategies, establishing: no-take marine reserves, regulated fishing zones, and unregulated open-access areas. We develop a general model that maximizes standing fish biomass, given a fixed management budget while maintaining a minimum harvest level. We find that when management budgets are small, sea-sparing is the optimal management strategy because for all parameters tested, reserves are more cost-effective at increasing standing biomass than traditional fisheries management. For larger budgets, the optimal strategy switches to sea-sharing because, at a certain point, further investing to grow the no-take marine reserves reduces catch below the minimum harvest constraint. Our intention is to illustrate how general rules of thumb derived from plausible, single-purpose models can help guide marine protected area policy under our novel sparing and sharing framework. This work is the beginning of a basic theory for optimal zoning allocations and should be considered complementary to the more specific spatial planning literature for marine reserve as nations expand their marine protected area estates.

Keywords Sparing vs sharing · Marine protected areas · Fisheries management · Marine zoning · Open-access fisheries · Marine policy

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Introduction

The land-sparing versus land-sharing (sparing vs sharing) debate emerged from contrasting views about how to balance the competing demands for biodiversity persistence and food production in agricultural landscapes (Green et al. 2005; Fischer et al. 2014). Land sparing involves spatial consolidation and intensification of agricultural activities. This approach is based on the idea that concentrated agricultural activity can achieve equal or higher yields in a smaller land area than low intensity usage. More land is available for biodiversity protection thereby providing a net conservation benefit. The counter-argument in support of sharing argues that wildlife-friendly farming produces lower yields per unit area, but supports biodiversity conservation by using less intensive production techniques across larger portions of the landscape (Fischer et al. 2008). Studies typically investigate the sparing vs. sharing dichotomy to identify the most appropriate strategy for a given context, because how well species or populations fare alongside increasing agricultural yields depends upon species traits and local production methods (Balmford et al. 2005; Green et al. 2005; Phalan et al. 2011; Grau et al. 2013). Although much of the debate centers around semantic issues (Tscharntke et al. 2012; Fischer et al. 2014), more recent empirical research supports the discussion with quantitative data (Lee et al. 2014; Butsic and Kuemmerle 2015; Kremen 2015; Law and Wilson 2015) particularly in plantation and livestock production (Grau et al. 2013).

While not framed as sparing vs. sharing per se, equivalent discussions in ocean management debate the benefits of either prohibiting fishing in some parts of the seascape or constraining fishing through management (White and Kendall 2007; Hilborn 2016). Marine reserves that exclude all extractive activities are a popular tool for conserving marine biodiversity. Efforts are underway to increase the number of reserves globally, particularly in developing countries where inshore fisheries experience heavy exploitation (White et al. 2014). In contrast, it is argued that traditional fisheries management, such as catch and size regulations, are more effective mechanisms to maintain healthy fish stocks and productive fisheries (Hilborn et al. 2004). In this context, quantitative investigations about sparing vs sharing in the sea traditionally argue whether or not marine reserves will provide greater fish biomass and environmental benefits than fishery regulations (Hastings and Botsford 1999; Hilborn et al. 2006; White and Kendall 2007)—a typically either/or argument. These studies identify whether a fraction of the system in marine reserves—sparing—or regulation across the entire area—sharing—maximizes fishery yields or profits (Sanchirico and Wilen 2001; Gerber et al. 2003; Hastings and Botsford 2003; Sanchirico et al. 2006; White et al. 2008). We note, however, there is a body of literature that considers and tests the utility of marine reserves as part of a mixed management strategy to achieve fisheries objectives, rather than an either/or argument (Holland and Brazee 1996; Mangel 2000; White et al. 2010).

Valid concerns remain regarding the socioeconomic impacts of marine reserves on communities and countries. Indeed, most studies modeling the use of reserves for fisheries management have found that the addition of reserves will reduce yields whenever fisheries are already well managed (Tuck and Possingham 2000; Hilborn et al. 2006), or suggest reserves are an effective secondary management option in cases where fisheries are heavily exploited or where effort reductions are unlikely to succeed (Holland and Brazee 1996). The establishment of marine reserves can lead to a redistribution of fishing effort within a region, potentially negating any net benefit of the reserve through increased fishing pressure elsewhere (Agardy et al. 2011). Other studies have identified scenarios in which reserves could be essential for maintaining high yields in spite of otherwise effective management regulations. These include, for example, the potentially critical function of reserves as a buffer against environmental stochasticity (Mangel 2000; West et al. 2009), and the positive impact of reserves on the density-dependent survival of young fish (White 2009) which could increase the net productivity of fished populations adjacent to reserves (but see White et al. 2008; Hart and Sissenwine 2009; Russ and Alcala 2011).

Similar to the terrestrial debate, there is no standard solution to protecting biodiversity and meeting human needs from the sea. Equipping decision-makers with a variety of tools to inform policy will enable better and more flexible management strategies as to which zoning allocation should be pursued in a given context. Australia's Great Barrier Reef Marine Park, for example, represents one of the first systematically designed networks of marine protected areas in the world whose shared seascape consists of roughly equal proportions of marine reserves, managed fisheries and general use areas (Fernandes et al. 2005). While successful in Australia (McCook et al. 2010), encouraging other countries to adopt the exact same allocation would be unfounded given the diverse ecological, socioeconomic, and governance structures across marine jurisdictions globally. Yet, general ecological and socioeconomic principles apply everywhere, and rules of thumb based on plausible, single-purpose models can help guide policy (Starfield 1997; Gerber et al. 2003) in a time of rapid marine protected area expansion (Klein et al. 2015).

Here, we transfer the land sparing vs. sharing debate to the sea using three common zoning types: fully protected no-take marine reserves, managed fishing zones, and unregulated and/or unmanaged fishing zones, hereafter called "open-access." We choose to characterize an allocation with only marine reserves and open-access areas as a "pure" sea sparing strategy. In the sea, we translate sharing to be any strategy that incorporates managed fishing zones, which can manifest as regulations on spatial or temporal effort, or gear restrictions that minimize impact to the benthos or non-target species. We characterize sharing along a continuum where some proportion of the seascape is managed, but consider a "pure" sharing strategy to be when the entire seascape is managed and no reserves or open-access zones exist (Fig. 1). When defined in this manner, we move beyond the sparing vs sharing dichotomy that prevails in the terrestrial debate (Kremen 2015), to develop a framework that includes seven potential spared and/or shared seascapes. We then illustrate how to operationalize the framework using a simple modeling approach whose optimally zoned seascapes secure a minimum biomass yield while maximizing standing stock biomass (the environmental benefit) for a given management budget. This approach considers a single habitat-dependent fished species whose harvest methods exert different levels of pressure on the benthos. We are interested in the circumstances in which the optimal seascape is either a sparing strategy, defined here when the case study area is allocated among no-take reserves and open-access zones, and when that changes to a sharing strategy, defined when the case study includes a managed fishery zone, and potentially the addition of either or both no-take and/or open-access zones (Fig. 1).

Material and methods

Model description

Our model assumes we are managing a single habitat-dependent fished species that reproduces with a pelagic larval phase leading to evenly distributed recruitment in all parts of the seascape. The seascape is divided into three management zones: protected marine reserves (fraction R), managed fishing zones (fraction M), and open-access fishing zones (fraction F; so every part of the system is in one of the zones, $R + M + F = 1$). There is a financial cost to reserving (C_R) and managing (C_M) habitat, the sum total of which must not exceed an allotted total management budget (B), $R*C_R + M*C_M \leq B$. We assume there is no management cost incurred in the open-access zone. Our objective is to maximize the total population of our fishery species subject to the budget constraint and a minimum biomass yield. Our model identifies the optimum proportional allocation of a seascape among the three zones.

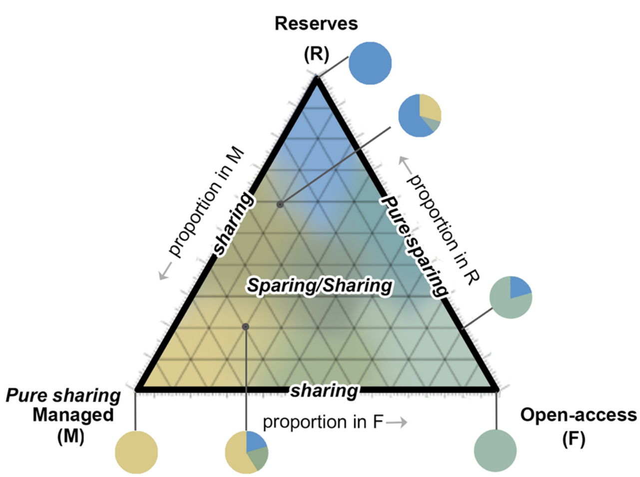

Fig. 1 Classes of sparing and sharing seascapes derived from our three-zone framework. Pure spared seascapes are those defined by no-take reserves (R) and open-access areas (F) and defined in these plots as any point on the line between F and R (excluding apex points where the zoning allocation would be 100%). Shared seascapes are defined by any allocation with managed fishing zones (M), with a pure shared seascape defined by apex M (100% managed). Pie charts offer illustrative examples to help interpret the zone allocation at given points on the graph

To link the decisions about seascape zoning allocation to our objectives and constraints, we use a simple population model tracking adult post-harvest biomass, A_t, at time t. Let L and K, be fecundity and the total number of potential sites available for larval settlement (i.e., larval carrying capacity), respectively. Fishing mortality in the managed and open-access zones are (1-S_M) and (1-S_F), respectively. We assume habitat damage temporarily reduces the proportion of available sites for settlement in zone type i, by D_i, for i in $\{M, F, R\}$, at time t. We assume the damage is more severe in the open-access zone ($D_M < D_F$), and that no habitat damage occurs in the no-take reserves, ($D_R = 0$). Assuming fish reproduce post-harvest and contribute larva to a common pool, which are then allocated to the three zone types proportionally based on area, we obtain the following difference equation for total post-harvest population size

$$A_{t+1} = \frac{[S_M(1-D_M)M + S_F(1-D_F)F + R]LA_t}{1 + LA_t/K}. \tag{1}$$

This formula is derived by assuming that larva uniformly settle at random among a fraction of available sites, which yields a Beverton-Holt recruitment relationship of the above form (Duncan et al. 2009).

The model has a stable equilibrium at

$$A^* = \left[S_M(1-D_M)M + S_F(1-D_F)F + R - \frac{1}{L}\right]K, \tag{2}$$

and analogous equilibrium harvest

$$H^* = \frac{[(1-S_M)(1-D_M)M + (1-S_F)(1-D_F)F]LA^*}{1 + LA^*/K}. \tag{3}$$

For simplicity, we assume 100% adult mortality after harvest and reproduction, but acknowledge the lifecycle for many short-lived species may not be annual. We then search through all financially possible zoning configurations to find the optimal seascape at equilibrium. The optimal solution is the seascape allocation that delivers the largest environmental benefit (total equilibrium post-harvest adult population size), while meeting the minimum harvest and budget constraints.

Ignoring the catch constraint we obtain an analytic solution for this optimal zoning allocation, which produces a general rule of thumb which holds true for small budgets (see "Results"). However, to account for the nonlinear catch constraint, we solved for the optimal allocation using simulations conducted in Matlab (MathWorks, Natick Massachusetts, USA; Appendix A).

Case study parameterization

For our case study, we apply our model to derive an optimum zone allocation based on the conditions of tiger prawn fisheries (O'Neill and Turnbull 2006) using the parameters outlined in Table 1. Damage caused by benthic fishing is difficult to quantify and depends on the type of gear, and the frequency and distribution of effort (Thrush et al. 1998; Collie et al. 2000). Impacts to coastal habitats range from diminished structural complexity (Auster 1998), changes to community composition (Thrush et al. 1998), and altered ecological processes (e.g., reduced primary production from macrofauna depletion; enhanced nutrient cycling via suspended sediment loads (Auster and Langton 1999)).

For the purpose of this exercise, we make several necessary simplifying assumptions about benthic impacts from fishing activities. We recognize benthic habitat condition is case-specific. In cases where more detailed data exist, this information can easily be incorporated into our modeling framework. We assume that previously unregulated trawling has impacted the benthic community in the open-access zone. We define impact as the mean mortality (20–50%) of benthic invertebrates reported in Collie et al. (2017) for towed benthic fishing gears. We assume perfectly enforced restrictions in the managed zone reduce the fishing impacts on the benthos by half so that $D_M = 0.5{*}D_F$ (Chuenpagdee et al. 2003). We set S_M to be the survival proportion that will yield MSY in a fully managed seascape and S_F to be the survival that leads to an equilibrium of 10% of virgin biomass when the fishery is completely unregulated, open access. We assume that fishers will not tolerate a level of catch lower than the pre-managed open access yield therefore the catch threshold (*CT*) is set to the open-access harvest.

Costs

Despite being critical to decision-making about natural resource management (Naidoo et al. 2006), costs associated with establishing and managing protected areas are often poorly reported, difficult to quantify (Balmford et al. 2004; Ban et al. 2011), and highly contextual (Rojas-Nazar et al. 2015). As a flexible way to integrate the amalgam of costs (e.g., stock assessments, ecological monitoring, staffing, enforcement, etc.) associated with the different zones (Ban et al. 2011) and across regions, we parameterize the relative costs between protected and managed areas. One key factor driving the cost of management interventions, be they marine reserves or gear restrictions, is the cost of enforcing compliance. The costs associated with surveillance and enforcement depend on both the size of the zones and the social and economic characteristics of the resource users. Only a few studies have explicitly quantified these costs (Ban and Klein 2009; Davis et al. 2015). Ban et al. (2011) compared the enforcement costs for staffing an entirely no-take protected area versus a mixed zone seascape (protected and fished) and found that compliance staffing was doubled when mixed zoning occurred.

As a starting point for our case study, we assume the cost of enforcing fisheries management is twice that of protecting area, $C_M = 2C_R$ but we test the sensitivity of the outcome to variations in the relative costs to protect and manage when

Table 1 Case study parameters based on population conditions for *Penaeus esculentus* (tiger prawn)

Parameter	Description	Value	Source
s	Intrinsic survival	1	O'Neill and Turnbull 2006
K	Carrying capacity of whole environment	30	O'Neill and Turnbull 2006
L*	Fecundity of adults	5	O'Neill and Turnbull 2006
D_F*	Habitat damage in the open-access fishing zone	0.35	Collie et al. 2017
D_M	Habitat damage in the managed fishing zone	0.175	(derived as $0.5{*}D_F$) Chuenpagdee et al. 2003
S_F*	Survivorship in fished zones	0.48	To achieve 10% virgin biomass at equilibrium. See formula in code, Appendix A
S_M	Survivorship in managed zones	0.65	To achieve MSY at equilibrium. See formula in code, Appendix A
CT*	Catch threshold	1.85	Open-access equilibrium
C_M to C_P*	Cost ratio between managing and protection	2:1	Ban et al. 2011

*Sensitivity tested (see Fig. 3 and Appendix)

$C_R = C_M$ and when the cost of enforcing reserves is double the cost of enforcing managed fishing areas $C_R = 2C_M$. We also examine the case of additional fixed costs (e.g., costs that do not scale with area) of reserves and managed areas in the appendix (see Appendix B). Management budgets can vary enormously between regions and in time; therefore, we are most interested in identifying the circumstances under which the optimal management strategy shifts between sparing and sharing as the management budget changes. We investigate the optimal strategy under different budgets to variations in several parameters of interest: habitat damage in the open-access fishing zone (D_F), escapement in the open-access fishing zone (S_F), fecundity (L), and the catch threshold (CT).

Results

Case study

If there is no management budget, then fishing must occur under open-access conditions throughout the seascape, regardless of the fishery being considered, because managed areas and reserves require financial investment. In our case study, we find that when management budgets are low (Fig. 2 where $B \leq 0.61$), the optimal choice is to allocate the entire budget to establishing no-take zones and have no managed areas. With the budget exhausted the rest of the seascape remains in open-access fishing—considered here as a sea sparing strategy where the portions of the seascape not under protection are intensively harvested. As the budget increases, so does the fraction of the protected seascape. During this stage, initially, the catch increases because additional reserves increase larvae production, which is then mostly distributed to unregulated zones for fishing. However, after a critical reserve threshold, catch declines because additional reserves do not provide sufficient larval export to the open-access zones to compensate the fishery for the population now excluded from harvesting. Eventually, the optimal seascape switches from sparing (reserves and open-access) to include all three zones—a version of sea sharing (Fig. 1). This occurs when further expanding the reserved area prevents the fishery from satisfying the minimum harvest constraint. In this case, biomass can be increased further with the addition of managed zones while still meeting the catch constraint.

Figure 3 shows how the optimal zoning allocation changes as a function of the budget for our parameters of interest: D_F, S_F, L, and CT. Beginning with no budget, the seascape is completely open-access fishing (apex F). As the budget grows, the allocation moves along the "sparing" boundary, where the seascape consists of open-access and increasing proportions of no-take reserves. A point of departure, or transition point, finally moves the allocation away from sea sparing and into a shared configuration consisting of all three zones. We find this departure is most sensitive to changes in fecundity (L) and occurs when the reserve coverage is between 45 and 70% of the seascape. When fecundity is greater, we switch to investing in management zones at lower proportions of reserves in the seascape.

Regardless of the parameter tested, we consistently observe the phenomenon of sea sparing when budgets are small, as well as the switch to the three-zone version of sharing as budgets increase. This trend is robust to changes in the cost ratio as well as when we eliminate the influence of habitat damage caused by fishing in each zone ($D_M = 0$ and $D_F = 0$) (see Appendix B–C for further sensitivity analyses). Sensitivity manifests in two possible ways that affect the optimal seascape as the budget grows: (1) the point of departure from sparing to sharing and (2) the proportion allocated to each zone (Fig. 3). Interestingly, the proportion of area protected, R, at the point of departure from sparing to sharing remains fairly constant irrespective of the cost ratio for our case study (Appendix B; about 60% of the seascape). When the cost of protection is double the cost of management, C_R=2C_M, the point of departure is substantially delayed as the budget grows large enough to share the seascape but ultimately follows the same investment strategy.

Optimal rule of thumb for small budgets

Our approach also allows us to derive an analytic rule of thumb to assist decision-makers about what the optimal investment strategy may be for their given context. With no catch constraint, the optimal zoning solution is to allocate the entire budget to marine reserves (sparing) if the benefit of adding a reserve (relative to open-access fishing), per unit cost, is greater than the cost-benefit of adding a managed area. Otherwise, the decision-maker should spend their entire budget on managed areas. This rule can be simplified mathematically as "spend the entire budget on reserves" if

$$1-\frac{1-S_M(1-D_M)}{1-S_F(1-D_F)} > \frac{C_M}{C_R}. \tag{4}$$

To derive this rule, let x be the amount of money allocated to reserves and, $B - x$, the amount of money allocated to managed areas. Then $R = x/C_R$ and $M = (B - x)/C_M$, and $F = 1 - R - M$. One can solve for the x that maximizes A^* by substituting these quantities into Eq. 2 which produces condition 4.

Based on our numerical simulations, the rule of thumb held for all tested cases until so many reserves had been purchased that the catch constraint would no longer be satisfied if the decision maker continued adding reserves. For our baseline parameterization, we found that reserves were favored over managed areas unless the cost of reserves was nearly five times that of managed areas. Even for the combination of

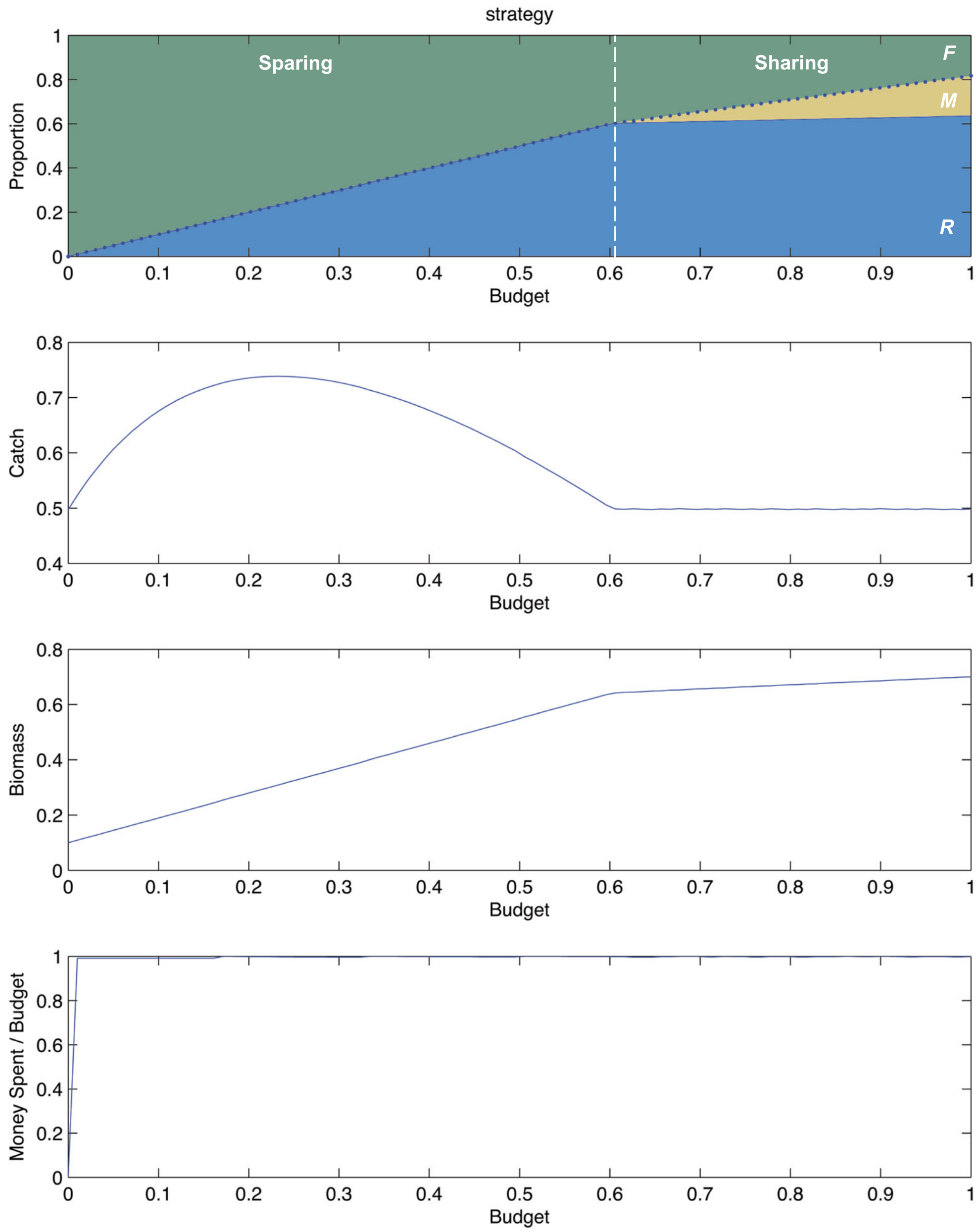

Fig. 2 The optimal sparing versus sharing strategy (top) showing the fraction of the seascape allocated to each of the three zones with an increasing budget for our case study. No-take marine reserves in blue (R); open-access fishing in green (F); and managed zones in yellow (M). The white dashed line is the departure point between sparing and sharing. When there is no budget we can neither reserve nor manage. As the budget increases, first marine reserves and then managed fisheries, enter the optimal zoning allocation. Also shown are catch, biomass, and the spending regime

parameters most favorable for managed areas in the sensitivity analysis, managed areas were not selected for low budgets unless the cost of reserves was over three times higher than the cost of managed areas.

Discussion

A sea sparing and sharing framework

Seven seascape allocations emerge from our sea sparing and sharing framework (Fig. 1). A seascape allocated entirely to one zone is highly unlikely as (1) an entirely reserved no-take system ($R = 1$) cannot meet the harvest constraint; (2) an unmanaged open-access system ($F = 1$) likely results in over exploitation and potential fishery collapse (Hutchings 2000); finally, while (3) a purely shared system is possible (e.g., $M = 1$ with no reserves or unmanaged fisheries), the reality of limited management budgets and global commitments to MPAs reduce the likelihood of this option persisting through time. Mixed zoning under our framework consists of (4) a pure spared seascape with both no-take reserves and open-access zones, (5) shared seascapes with managed and open-access zones, and two zoning configurations that allow "sparing and sharing." The first of these last two zoning configurations includes (6) no-take reserves and managed fisheries; and (7) no-take reserves, managed fisheries and open-access zones. With this conceptual starting point, a useful next

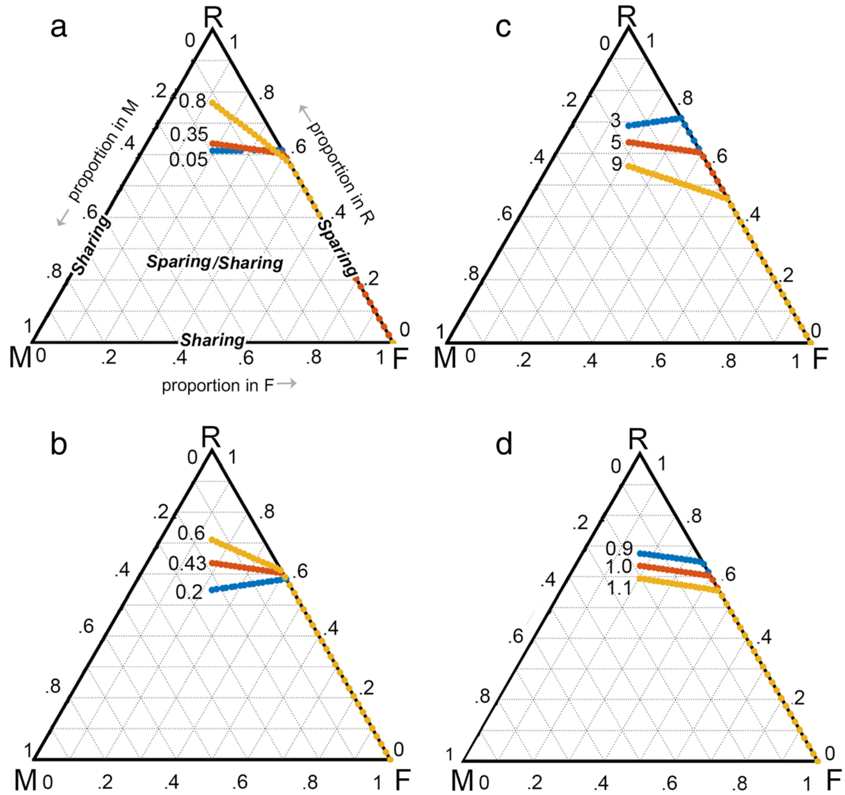

Fig. 3 Ternary plots showing the fraction of the seascape in each of the three zones (R = no take reserves, M = managed fishing zones, F = open access) for a given budget, where $R + M + F = 1$. When no budget exists, $B = 0$, the entire seascape is open access, 100% F in the bottom right corner. Colored lines show the sensitivity of the seascape allocation under several values for each parameter of interest: **a** habitat damage caused by fishing in the open-access fishing zone (D_F), **b** escapement in the open-access fishing zone (S_F), **c** fecundity of adults (L), and **d** the catch threshold (CT). The departure from the sparing strategy (line F–R) indicates the transition point from sparing to sharing as the budget increases

step for the future would be to classify existing management plans within this framework to see what the most dominant strategies are in practice, and to create a typology of spared and shared seascapes that enable moving beyond the dichotomous view of the sparing vs sharing debate. Building on this idea, our framing also exposes the need for a more refined classification system, as "sparing," "sharing," and "sparing and sharing" are too vague to encompass the nuanced management practices governing marine systems (White et al. 2010; Kremen 2015).

Only the rich can afford to share

When budgets are small, sea sparing is always the optimal allocation. As the budget grows, we arrive at a point where increasing the amount of the reserves any further will compromise our ability to achieve the minimum harvest constraint. If budgets increase beyond this point, the optimal strategy is to start sharing. The optimal strategy under our framework will be specific to the definition of objectives and constraints (White et al. 2017). For example, we approached this problem by identifying a single conservation objective (maximize standing biomass), while acknowledging two constraints: a natural resource requirement (expressed by the minimum harvest constraint) and a fixed management budget. However, it is important to note there are many alternate ways to frame this problem depending on whether the above outcome variables are treated as objectives to be maximized or minimized, and/or constraints. Defining a different objective for ocean management (e.g., maximizing larval connectivity, protecting species climate refugia (Beger et al. 2015) or building near-pristine fish biomass (McClanahan et al. 2007)), or evaluating trade-offs for multi-objective problems would also be valid approaches.

We strategically simplify many assumptions in order to develop a model that can begin to inform policy (Hastings and Botsford 1999). Opportunities to add complexity into our approach include incorporating a spatially realistic modeling environment (Polasky et al. 2008; Metcalfe et al. 2015), alternative assumptions of density dependence before and after settlement (e.g. Ricker models), age structure, overcompensation (e.g., White and Kendall (2007)), integrating more complex dispersal processes, accounting for variable distributions of fishing effort and displacement, socioeconomics (Sanchirico and Wilen 2002; Halpern et al. 2004; Armstrong and Skonhoft 2006; Costello and Polasky 2008), and developing multi-species models.

For some of these limitations, we can foresee how the model will respond. For example, adding age structure would allow biomass to accumulate in reserves, likely achieving our objectives with less reserved area. In instances where overcompensation is justified we would expect to see higher reserve coverage (White and Kendall 2007). We acknowledge that our approach also depends on some degree of overfishing for this framework to apply. This assumption influences the point of departure, in that, the time at which managed areas are added will depend on the assumptions of overfishing. However, the general trend of sparing first and moving to the three-zone version of sharing is robust and highlights that mixed management approaches have merit where substantial management capacity exists (Hilborn 2016).

The species and associated fishery we chose to represent in the model are intentionally responsive to reserves, because we believe that it is these types of species and fisheries that drive zoning decisions for coastal management. However, our findings may also apply to systems where common pool dispersal assumptions are not met. The first empirical measurements of larval dispersal revealed unexpectedly high levels of self-recruitment (Jones et al. 1999; Swearer et al. 1999) which challenged the general assumption of strong population connectivity across large seascapes. More recent studies confirm that larval settlement close to spawning locations is indeed common, but that the dispersal distances of a significant proportion of other larvae can still be extensive (Green et al. 2015; Jones 2015; Williamson et al. 2016; Almany et al. 2017). In such cases, reserve size and placement can be optimized with a high level of flexibility to provide for maximum fishery benefits (Krueck et al. 2017a, b).

Despite our stated limitations, our model goes beyond traditional management zone assessments by illustrating how fisheries management influences the optimal seascape allocation. Our approach is the first attempt to underpin the sharing and sparing debate with a process model. In doing so, we reveal a more nuanced and practical framework than the debate has produced to date (Kremen 2015). Ocean management can benefit from applying this framework and devising simple rules of thumb to guide policy options, for example, investing in marine reserves when budgets are low with the addition of managed areas when budgets are high. Building additional complexity into this base exploration as well as developing the sea sparing vs sea sharing framework will help advance the debate and its relevance for marine policy. This work is the beginning of a basic theory for optimal allocations within seascape zoning frameworks and should be considered complementary to the more specific spatial planning literature for marine reserve design and implementation, which addresses the size, shape, and placement of individual MPAs within a seascape.

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References

Agardy T, di Sciara GN, Christie P (2011) Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. Mar Policy 35(2):226–232. https://doi.org/10.1016/j.marpol.2010.10.006

Almany GR, Planes S, Thorrold SR, Berumen ML, Bode M, Saenz-Agudelo P, Bonin MC, Frisch AJ, Harrison HB, Messmer V (2017) Larval fish dispersal in a coral-reef seascape. Nat Ecol Evol 1:s41559–s41017

Armstrong CW, Skonhoft A (2006) Marine reserves: a bio-economic model with asymmetric density dependent migration. Ecol Econ 57(3):466–476. https://doi.org/10.1016/j.ecolecon.2005.05.010

Auster PJ (1998) A conceptual model of the impacts of fishing gear on the integrity of fish habitats. Conserv Biol 12(6):1198–1203. https://doi.org/10.1046/j.1523-1739.1998.0120061198.x

Auster PJ, Langton RW (1999) The effects of fishing on fish habitat. In: Benaka L (ed) Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Bethesda, p 150–187

Balmford A, Gravestock P, Hockley N, McClean CJ, Roberts CM (2004) The worldwide costs of marine protected areas. Proc Natl Acad Sci USA **101**:9694–9697

Balmford A, Green R, Scharlemann JPW (2005) Sparing land for nature: exploring the potential impact of changes in agricultural yield on the area needed for crop production. Glob Chang Biol 11(10):1594–1605. https://doi.org/10.1111/j.1365-2486.2005.001035.x

Ban NC, Klein CJ (2009) Spatial socioeconomic data as a cost in systematic marine conservation planning. Conserv Lett 2(5):206–215. https://doi.org/10.1111/j.1755-263X.2009.00071.x

Ban NC, Adams V, Pressey RL, Hicks J (2011) Promise and problems for estimating management costs of marine protected areas. Conserv Lett 4(3):241–252. https://doi.org/10.1111/j.1755-263X.2011.00171.x

Beger M, McGowan J, Treml EA, Green AL, White AT, Wolff NH, Klein CJ, Mumby PJ, Possingham HP (2015) Integrating regional conservation priorities for multiple objectives into national policy. Nat Commun 6:8208. https://doi.org/10.1038/ncomms9208

Butsic V, Kuemmerle T (2015) Using optimization methods to align food production and biodiversity conservation beyond land sharing and land sparing. Ecol Appl 25(3):589–595. https://doi.org/10.1890/14-1927.1

Chuenpagdee R, Morgan LE, Maxwell SM, Norse EA, Pauly D (2003) Shifting gears: assessing collateral impacts of fishing methods in US waters. Front Ecol Environ 1(10):517–524

Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. J Anim Ecol 69(5):785–798. https://doi.org/10.1046/j.1365-2656.2000.00434.x

Collie J, Hiddink JG, Kooten T, Rijnsdorp AD, Kaiser MJ, Jennings S, Hilborn R (2017) Indirect effects of bottom fishing on the productivity of marine fish. Fish Fish 18(4):619–637. https://doi.org/10.1111/faf.12193

Costello C, Polasky S (2008) Optimal harvesting of stochastic spatial resources. J Environ Econ Manag 56(1):1–18. https://doi.org/10.1016/j.jeem.2008.03.001

Davis K, Kragt M, Gelcich S, Schilizzi S, Pannell D (2015) Accounting for enforcement costs in the spatial allocation of marine zones. Conserv Biol 29(1):226–237. https://doi.org/10.1111/cobi.12358

Duncan RP, Diez JM, Sullivan JJ, Wangen S, Miller AL (2009) Safe sites, seed supply, and the recruitment function in plant populations. Ecology 90(8):2129–2138. https://doi.org/10.1890/08-1436.1

Fernandes L, Day JON, Lewis A, Slegers S, Kerrigan B, Breen DAN, Cameron D, Jago B, Hall J, Lowe D, Innes J, Tanzer J, Chadwick V, Thompson L, Gorman K, Simmons M, Barnett B, Sampson K, De'Ath G, Mapstone B, Marsh H, Possingham H, Ball IAN, Ward T, Dobbs K, Aumend J, Slater DEB, Stapleton K (2005) Establishing representative no-take areas in the great barrier reef: large-scale implementation of theory on marine protected areas. Conserv Biol 19(6):1733–1744. https://doi.org/10.1111/j.1523-1739.2005.00302.x

Fischer J, Brosi B, Daily GC, Ehrlich PR, Goldman R, Goldstein J, Lindenmayer DB, Manning AD, Mooney HA, Pejchar L (2008) Should agricultural policies encourage land sparing or wildlife-friendly farming? Front Ecol Environ 6(7):380–385. https://doi.org/10.1890/070019

Fischer J, Abson DJ, Butsic V, Chappell MJ, Ekroos J, Hanspach J, Kuemmerle T, Smith HG, von Wehrden H (2014) Land sparing versus land sharing: moving forward. Conserv Lett 7(3):149–157. https://doi.org/10.1111/conl.12084

Gerber LR, Botsford LW, Hastings A, Possingham HP, Gaines SD, Palumbi SR, Andelman S (2003) Population models for marine reserve design: a retrospective and prospective synthesis. Ecol Appl 13(sp1):47–64

Grau R, Kuemmerle T, Macchi L (2013) Beyond 'land sparing versus land sharing': environmental heterogeneity, globalization and the balance between agricultural production and nature conservation. Curr Opin Environ Sustain 5(5):477–483. https://doi.org/10.1016/j.cosust.2013.06.001

Green RE, Cornell SJ, Scharlemann JPW, Balmford A (2005) Farming and the fate of wild nature. Science 307(5709):550–555. https://doi.org/10.1126/science.1106049

Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, Gleason MG, Mumby PJ, White AT (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol Rev 90(4):1215–1247. https://doi.org/10.1111/brv.12155

Halpern BS, Gaines SD, Warner RR (2004) Confounding effects of the export of production and the displacement of fishing effort from marine reserves. Ecol Appl 14(4):1248–1256. https://doi.org/10.1890/03-5136

Hart DR, Sissenwine MP (2009) Marine reserve effects on fishery profits: a comment on White et al. (2008). Ecol Lett 12(3):E9–E11. https://doi.org/10.1111/j.1461-0248.2008.01272.x

Hastings A, Botsford LW (1999) Equivalence in yield from marine reserves and traditional fisheries management. Science 284(5419):1537–1538. https://doi.org/10.1126/science.284.5419.1537

Hastings A, Botsford LW (2003) Comparing designs of marine reserves for fisheries and for biodiversity. Ecol Appl 13(sp1):65–70

Hilborn R (2016) Marine biodiverity needs more than protection. Nature 535(7611):224–226. https://doi.org/10.1038/535224a

Hilborn R, Stokes K, Maguire JJ, Smith T, Botsford LW, Mangel M, Orensanz J, Parma A, Rice J, Bell J, Cochrane KL, Garcia S, Hall SJ, Kirkwood GP, Sainsbury K, Stefansson G, Walters C (2004) When can marine reserves improve fisheries management? Ocean Coast Manag 47(3-4):197–205. https://doi.org/10.1016/j.ocecoaman.2004.04.001

Hilborn R, Micheli F, De Leo GA (2006) Integrating marine protected areas with catch regulation. Can J Fish Aquat Sci 63(3):642–649. https://doi.org/10.1139/f05-243

Holland DS, Brazee RJ (1996) Marine reserves for fisheries management. Mar Resour Econ 11(3):157–171. https://doi.org/10.1086/mre.11.3.42629158

Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406(6798):882–885. https://doi.org/10.1038/35022565

Jones GP (2015) Mission impossible: unlocking the secrets of coral reef fish dispersal. In: Mora C (ed) Ecology of fishes on coral reefs, Cambridge University Press, Cambridge, p 16–28

Jones GP, Milicich MJ, Emslie MJ, Lunow C (1999) Self-recruitment in a coral reef fish population. Nature 402(6763):802–804. https://doi.org/10.1038/45538

Klein CJ, Brown CJ, Halpern BS, Segan DB, McGowan J, Beger M, Watson JEM (2015) Shortfalls in the global protected area network at representing marine biodiversity. Sci Rep 5(1):17539. https://doi.org/10.1038/srep17539

Kremen C (2015) Reframing the land-sparing/land-sharing debate for biodiversity conservation. Ann N Y Acad Sci 1355(1):52–76. https://doi.org/10.1111/nyas.12845

Krueck NC, Ahmadia GN, Green A, Jones GP, Possingham HP, Riginos C, Treml EA, Mumby PJ (2017a) Incorporating larval dispersal into MPA design for both conservation and fisheries. Ecol Appl 27(3):925–941. https://doi.org/10.1002/eap.1495

Krueck NC, Ahmadia GN, Possingham HP, Riginos C, Treml EA, Mumby PJ (2017b) Marine reserve targets to sustain and rebuild unregulated fisheries. PLoS Biol 15(1):e2000537. https://doi.org/10.1371/journal.pbio.2000537

Law, E. A. and K. A. Wilson (2015) Providing context for the land-sharing and land-sparing debate. Conserv Lett 8(6):404–413. https://doi.org/10.1111/conl.12168

Lee JSH, Garcia-Ulloa J, Ghazoul J, Obidzinski K, Koh LP (2014) Modelling environmental and socio-economic trade-offs associated with land-sparing and land-sharing approaches to oil palm expansion. J Appl Ecol 51(5):1366–1377. https://doi.org/10.1111/1365-2664.12286

Mangel M (2000) On the fraction of habitat allocated to marine reserves. Ecol Lett 3(1):15–22. https://doi.org/10.1046/j.1461-0248.2000.00104.x

McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA (2007) Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecol Appl 17(4):1055–1067. https://doi.org/10.1890/06-1450

McCook LJ, Ayling T, Cappo M, Choat JH, Evans RD, De Freitas DM, Heupel M, Hughes TP, Jones GP, Mapstone B (2010) Adaptive management of the great barrier reef: a globally significant demonstration of the benefits of networks of marine reserves. Proceedings of the National Academy of Sciences **107**:18278–18285

Metcalfe K, Vaz S, Engelhard GH, Villanueva MC, Smith RJ, Mackinson S (2015) Evaluating conservation and fisheries management strategies by linking spatial prioritization software and ecosystem and fisheries modelling tools. J Appl Ecol 52(3):665–674. https://doi.org/10.1111/1365-2664.12404

Naidoo R, Balmford A, Ferraro PJ, Polasky S, Ricketts TH, Rouget M (2006) Integrating economic costs into conservation planning. Trends Ecol Evol 21(12):681–687. https://doi.org/10.1016/j.tree.2006.10.003

O'Neill MF, Turnbull C (2006) Stock assessment of the Torres Strait tiger prawn fishery (*Penaeus esculentus*). Department of Primary Industries and Fisheries, Brisbane City

Phalan B, Onial M, Balmford A, Green RE (2011) Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science 333(6047):1289–1291. https://doi.org/10.1126/science.1208742

Polasky S, Nelson E, Camm J, Csuti B, Fackler P, Lonsdorf E, Montgomery C, White D, Arthur J, Garber-Yonts B (2008) Where to put things? Spatial land management to sustain biodiversity and economic returns. Biol Conserv 141(6):1505–1524. https://doi.org/10.1016/j.biocon.2008.03.022

Rojas-Nazar UA, Cullen R, Gardner JPA, Bell JJ (2015) Marine reserve establishment and on-going management costs: a case study from New Zealand. Mar Policy 60:216–224. https://doi.org/10.1016/j.marpol.2015.06.029

Russ GR, Alcala AC (2011) Enhanced biodiversity beyond marine reserve boundaries: the cup spillith over. Ecol Appl 21(1):241–250. https://doi.org/10.1890/09-1197.1

Sanchirico JN, Wilen JE (2001) A bioeconomic model of marine reserve creation. J Environ Econ Manag 42(3):257–276. https://doi.org/10.1006/jeem.2000.1162

Sanchirico JN, Wilen JE (2002) The impacts of marine reserves on limited-entry fisheries. Nat Resour Model 15:291–310

Sanchirico JN, Malvadkar U, Hastings A, Wilen JE (2006) When are no-take zones an economically optimal fishery management strategy? Ecol Appl 16(5):1643–1659

Starfield AM (1997) A pragmatic approach to modeling for wildlife management. J Wildl Manag 61(2):261–270. https://doi.org/10.2307/3802581

Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. Nature 402(6763):799–802. https://doi.org/10.1038/45533

Thrush SF, Hewitt JE, Cummings VJ, Dayton PK, Cryer M, Turner SJ, Funnell GA, Budd RG, Milburn CJ, Wilkinson MR (1998) Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. Ecol Appl 8(3):866–879

Tscharntke T, Clough Y, Wanger TC, Jackson L, Motzke I, Perfecto I, Vandermeer J, Whitbread A (2012) Global food security, biodiversity conservation and the future of agricultural intensification. Biol Conserv 151(1):53–59. https://doi.org/10.1016/j.biocon.2012.01.068

Tuck GN, Possingham HP (2000) Marine protected areas for spatially structured exploited stocks. Mar Ecol Prog Ser 192:89–101. https://doi.org/10.3354/meps192089

West CD, Dytham C, Righton D, Pitchford JW (2009) Preventing overexploitation of migratory fish stocks: the efficacy of marine protected areas in a stochastic environment. ICES J Mar Sci 66(9):1919–1930. https://doi.org/10.1093/icesjms/fsp159

White C (2009) Density dependence and the economic efficacy of marine reserves. Theor Ecol 2(3):127–138. https://doi.org/10.1007/s12080-009-0039-3

White C, Kendall BE (2007) A reassessment of equivalence in yield from marine reserves and traditional fisheries managament. Oikos 116(12):2039–2043. https://doi.org/10.1111/j.2007.0030-1299.16167.x

White C, Kendall BE, Gaines S, Siegel DA, Costello C (2008) Marine reserve effects on fishery profit. Ecol Lett 11(4):370–379. https://doi.org/10.1111/j.1461-0248.2007.01151.x

White JW, Botsford LW, Moffitt EA, Fischer DT (2010) Decision analysis for designing marine protected areas for multiple species with uncertain fishery status. Ecol Appl 20(6):1523–1541. https://doi.org/10.1890/09-0962.1

White AT, Aliño PM, Cros A, Fatan NA, Green AL, Teoh SJ, Laroya L, Peterson N, Tan S, Tighe S, Venegas-Li R, Walton A, Wen W (2014) Marine protected areas in the coral triangle: progress, issues, and options. Coast Manag 42(2):87–106. https://doi.org/10.1080/08920753.2014.878177

White JW, Nickols KJ, Botsford LW (2017) Response to O'Leary et al.: misuse of models leads to misguided conservation recommendations. Conserv Lett 10(2):269–270. https://doi.org/10.1111/conl.12344

Williamson DH, Harrison HB, Almany GR, Berumen ML, Bode M, Bonin MC, Choukroun S, Doherty PJ, Frisch AJ, Saenz-Agudelo P (2016) Large-scale, multidirectional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park. Mol Ecol 25(24):6039–6054. https://doi.org/10.1111/mec.13908