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The trade-off between biodiversity and sustainable fish harvest with area-based management

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While fisheries provide food and employment for hundreds of millions of people, they also can have significant impact on biodiversity. We explore the potential of area-based fisheries management to simultaneously maintain biodiversity and high levels of sustainable food production. We used two illustrative examples of fisheries that have different gear types, areas, and species to evaluate the trade-off between biodiversity and harvest. We calculate the optimal effort by gear and area that maximizes a weighted objective function of biodiversity and harvest, ranging from 100% of the weight on harvest to 100% on biodiversity. We found for both case studies that the trade-off was highly convex, with win-win solutions allowing for high levels of both fishery harvest and conservation. This is achieved by reducing or eliminating fishing effort that negatively impacts high conservation value species while maintaining fishing effort with gears and in areas where there is low conservation impact. We suggest that in most fisheries, such situations can be found, and that effective area-based management can provide for high levels of biodiversity protection and food production.

Keywords: area-based management, biodiversity, conservation trade-off, harvest.

Introduction

Fishery managers seek the optimal balance between two conflicting objectives: economics and conservation. In 2015 the United Nation's Sustainable Development Goals (SDG) were adopted by 193 nations. The SDG's aim to provide food security and improved nutrition (SDG 2), while also sustainably managing and protecting marine and coastal ecosystems (SDG 14.2). Harvesting marine fish contributes to both of these goals, and produces goods and services that 40 million people depend on for income (FAO, 2018) and much of the world for food. However, fishing also has negative impacts on

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biodiversity that can include reduced abundance of target and non-target species, impacts on benthic biota from bottom contact gear, and changes in marine food webs (Garcia, 1994). Societal objectives include both maximizing the benefits from fishing and minimizing the negative impacts of fishing on biodiversity (SDG 14.2).

Reducing the impact of fishing on biodiversity is increasingly recognized as an international objective, and 196 nations adopted the Aichi targets of the Convention on Biodiversity (CBD) (https://www.cbd.int/sp/targets/, accessed April 20, 2020), which aim to have 10% of coastal and marine areas "conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures." The CBD defines protected areas as "a geographically defined area, which is designated or regulated and managed to achieve specific conservation objectives" (Article 2 of the Convention). But what is the most effective mix of area-based management approaches to achieve societal objectives?

Area-based management is a central element in most conservation and fishery management approaches (Hilborn, 2011) and it may include no-take areas, prohibition of specific gears in certain areas, and, most commonly, regulation of fishing effort or catch by area. For example, in the federally managed fisheries of Alaska (Figure 1), all of these tools are used (https://www.npfmc.org/habitat-protections, accessed April 20, 2020). All Arctic waters are closed to fishing until management plans are developed. Most state waters and almost all federal waters in southeast Alaska are closed to bottom trawling as are large portions of the Aleutian Islands and the Bering Sea. Numerous areas around sea lion (*Eumetopias jubatus*) colonies are closed to all fishing, and species-specific catch is regulated by area. Nursery areas for crabs are closed.

The trade-offs resulting from area-based management have been explored across multiple forms of goods and services, including fisheries, wind energy, whale watching (White *et al.*, 2012), coral reef protection, and fisheries harvest (Brown and Mumby, 2014), and between fisheries yield and abundance of target species (Rassweiler *et al.*, 2014). In each case, a spatially explicit numerical model was used to evaluate the trade-off, which was usually found to be convex, meaning area-based management rules were found where you had both high catch and high biodiversity. In most regions of the world, there is a mix of different fishing gears and both target and non-target species, leading to many possible spatial configurations of area-based regulations.

There is considerable debate about the relative effectiveness of exclusive no-take areas compared with other forms of area-based management, which maintain biodiversity and permit exploitation. Lubchenco and Grorud-Colvert (2015) argue that only no-take marine protected areas (MPAs) constitute biodiversity protection, meaning that the area-based management seen in Alaska does not constitute protection nor meet the CBD targets – that only no-take marine protected areas (MPAs) constitute biodiversity protection (Lubchenco and Grorud-Colvert, 2015). However, Rice *et al.* (2018) argue that area-based management of fishing effort can provide biodiversity protection that does meet the CBD targets.

The trade-off between sustainable yield and abundance of fish stocks does emerge from both single-species and multispecies models. The logistic population model (Figure 2) shows a trade-off between population size and sustainable yield, as does an ensemble of EwE models (Worm *et al.*, 2009). These models serve as a baseline for considering the trade-off between biodiversity and sustainable harvest, using total abundance of fish as a

metric for biodiversity, but neither considers either multiple areas or multiple gears or bycatch species. In both cases, the convex trade-off allows for roughly 80% of the potential harvestable yield, while maintaining 70% of the biodiversity. Adding area-based management and gear management should generally improve the optimization of harvest and conservation.

We explore two case studies of the trade-off between biodiversity and fisheries yield using a spatially-explicit model that includes both target and bycatch species, and different gear types. The management options will be the allocation of effort by gear and area, so that no-take areas where all gears are prohibited is an option, whereas selective prohibition of gear by area is another option. We examine to what extent biodiversity can be maintained while sustainably harvesting fish stocks.

An immediate impediment to such an analysis is the lack of an operational definition of biodiversity. While we can use landed value as a quantitative measure of fisheries harvest performance, there are a wide range of measures of biodiversity, none of which are broadly accepted as preferred. Biodiversity concerns can be ranked by risk of extinction. Thus, species that are threatened with extinction are often given a high priority for protection, followed by charismatic species and overfished species. Breeding or nursery sites are also often given special protection, as are areas of particular cultural or recreational interest. If we examine the area-based management system of Alaska, we see each of these priorities addressed. Our approach is to define biodiversity as a weighted function of the relative abundance of each species, and to place high weights on species considered of high conservation value or concern. Any other definition of biodiversity could be evaluated within the modeling context so long as the species needed to calculate biodiversity are included within the model.

Methods

We designed a model that calculates the equilibrium abundance of each species by area, considering both target and bycatch species. The control variable is the amount of fishing effort allowed by fishing gear (or fishing method) and by area. The objective function is a weighted measure of biodiversity and fishing revenue. Initially, we calculate the trade-off between revenue and biodiversity by estimating the amount of effort by gear and by area to achieve maximum revenue. Then, in a gradual series of optimizations, we reduce the weighting on revenue and increase the weighting on biodiversity until the objective function is maximized only for biodiversity. The NLMINB function in the "stats" package in R (RCoreTeam, 2020) was used to do the optimization. In all cases, as a result of model assumptions, biodiversity is maximized when no fishing is allowed.

We assume the time dynamics of the populations are governed by the logistic growth equation with species and area subscripts omitted in equation (1), but included in equation (2). No trophic interactions are considered:

$$B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{k} \right) - u_t B_t$$

$$C_t = uB_t$$

$$u = \sum_g E_g q_g$$
(1)

The equilibrium abundance (B^*) for a species and area is thus:

$$B_{sa}^* = k_{sa} \left(\frac{r_{sa} - u_{sa}}{r_{sa}} \right) \tag{2}$$

We will assume the objective of fishing is to maximize total revenue (R), which is the sum across gears and areas of the revenue (R_{ga}) :

$$R = \sum_{qa} (R_{qa}) \tag{3}$$

The revenue is catch times price (p):

$$R_a = \sum_{s,a} B_{a,s}^* E_{a,a} q_{as} p_s \tag{4}$$

We will assume that the biodiversity objective (D) is the sum of the total biomass (B) of each species as a fraction of the unfished biomass times the "biodiversity value" (v) we place on each species. This allows us to place more weight on species of conservation concern

$$D = \sum_{S} \frac{\sum_{a} B_{S,a}^{*}}{\sum_{a} k_{S,a}} v_{S}$$
 (5)

The total value of the fishery (V) will be a weighted sum of the revenue (R) and the biodiversity (D). First we calculate the maximum value by optimizing profit with no value placed on diversity to find R_{max} , and then optimize biodiversity with no value placed on revenue (D_{max}):

$$V = w \frac{R}{R_{max}} + (1 - w) \frac{D}{D_{max}}$$
 (6)

Having calculated R_{max} and D_{max} , we then begin with w = 1 (all weight on revenue) and calculate the optimal allocation of effort by gear and area and resulting revenue and biodiversity, then step over values of w from 1 to 0 in increments of 0.01.

We include results for two representative case studies. Each of these should be considered illustrative. We have attempted to make the *r* biologically reasonable with long-lived species having a lower *r* ensuring their sustainable exploitation rate is lower than short-lived species. The interaction with non-target species are set to make sure that in the absence of weight on biodiversity, there would be considerable impact. This is not meant to represent the level of bycatch impact that actually occurs. The key element of the models is that each gear has a different impact on each species, and the distribution of species (especially those of most concern) is usually different between areas.

Bering Sea and Aleutian Islands

The species or groups are modeled after benthic corals and sponges, albatross (family Diomedeidae), fur seals (Callorhinus ursinus), walleye pollock (Gadus chalcogrammus), Pacific cod (Gadus macrocephalus), yellowfin sole (Limanda aspera), halibut (Hippoglossus stenolepis), and crabs (Chionoecetes spp. and Paralithodes spp.). We consider four fishing gears: (1) trawling which targets pollock, yellowfin sole, and Pacific cod, but also impacts corals/sponges and has a minor impact on albatross; (2) crab potting which we assume only impacts crabs; (3) longline which targets cod and halibut, but impacts albatross and has some impact on corals/sponges; and (4) seal harvesting, which is a directed fishery. We consider five areas (Figure 3a): (1) the Pribilof Islands where the fur seals breed and where minor stocks of the other species are found; (2) the inner Bering Sea which has most of the yellowfin sole, but also some pollock, cod, halibut, and crabs; (3) the middle Bering Sea which has all species except fur seals; (4) the outer Bering Sea which has most of the pollock and cod; and (5) the Aleutian Islands which have most of the species, but also most of the corals/sponges and many albatross. Values of the parameters are shown in Table S1 in the Supplementary material. We assign a biodiversity weight of 10 to corals/sponges, 5 to albatross and fur seals, and 1 to other species.

California coastal fishery

This model is styled after a range of fisheries off the coast of California in which there are five fishing gears: (1) bottom trawling targeting two high-value bottom fish – black cod (*Anoplopoma fimbri*) and halibut, but also has negative effects on vulnerable marine ecosystems (VME); (2) pot fishing catching black cod and crabs (*Metacarcinus magister*), with a slight impact on VMEs; (3) hook-and-line fishing catching black cod and halibut, with no impact on non-target species; (4) purse seining targeting squid (*Doryteuthis opalescens*), with an impact on birds and mammals; and (5) a dive fishery for sea urchins (*Mesocentrotus franciscanus*) that has no impact on any other species.

We consider five areas (Figure 3b): (1) regions around bird nesting sites that are key to bird foraging; (2) nearshore areas where mammals and VMEs are common, as are squid and urchins; (3) the north coast includes black cod, crab, urchins, and mammals, but no birds or VMEs; (4) the central coast includes black cod, halibut, crab, squid, mammals, and some VME; and (5) the south coast includes black cod, halibut, squid, urchins, mammals, and some VMEs. We assigned a biodiversity weight of 10 to the birds, mammals, and VMEs and a value of 1 to the other species. Parameters of this model are presented in Table S2 in the Supplementary material.

Results

Bering Sea and Aleutian Islands

When all the weight is placed on revenue from fishing, each targeted stock is maintained at or near the maximum sustainable yield (MSY) abundance, and the sensitive corals/sponges and albatross are extirpated (Figure 4a). Fur seals are at one-half of their carrying capacity (0.5k), which maximizes their sustainable yield. As soon as any weight is placed on biodiversity, trawling is closed in the Aleutian Islands, and at 10% weight,

longlining in the Aleutian Islands is also closed. These changes cause the corals and sponges to be at two-thirds of their carrying capacity (the other one-third of the corals/sponges are in the outer Bering Sea). Fur seal harvest is gradually reduced as the value of biodiversity increases. When the weight on biodiversity reaches 30%, longlining is closed in the outer Bering Sea to protect albatross. The next big jump in biodiversity occurs when trawling in the outer Bering Sea is closed and coral and sponge biodiversity increases while revenue plummets.

The overall trade-off is quite convex (Figure 4b) such that it is possible to achieve 87% of maximum revenue while maintaining biodiversity at 77%. In this example, high-value biodiversity species (corals and albatross) can be largely or even fully protected from bottom-contact gear (for corals), or eliminating the fishing gear that causes mortality (for albatross) by closing areas where these species occur. No-take areas that are closed to all fishing do not appear until the weight on biodiversity reaches over 90%. Crab potting is the last fishing gear to be totally eliminated, as it has no impact on the three primary species of biodiversity value in this model. Trawling is eliminated from the Aleutian Islands when there is any weight on biodiversity, from the Pribilof Islands when biodiversity weight is 42%, from the outer Bering Sea (where there are some corals and sponges) when biodiversity weight reaches 70%, and from the middle and inner Bering Sea when biodiversity weight reaches 90%.

California coastal fishery

When no value is assigned to biodiversity birds and mammals, VMEs are extirpated and target species are managed to produce maximum revenue (Figure 5a). As soon as value is assigned to biodiversity, all fishing except diving is closed in the bird nesting areas, and trawling is closed everywhere except the central region which has low VME abundance. The result is that biodiversity increases from 0.2 to 0.75 with almost no loss of revenue (Figure 5b) because pot fishing can harvest the black cod and hook-and-line fishing harvests the halibut. Mammals recover to a value of 0.4, but because they are affected by seine gear and are found in all areas, their abundance rises gradually as weight on biodiversity is increased and the intensity of seine fishing declines. When the weight on biodiversity is about 0.5, all seine fishing and trawling have ceased. Hook-and-line fishing continues in the south and central regions, and dive fishing everywhere except the central region (where there are no urchins) until biodiversity weight reaches 90%, at which time everything is closed to fishing.

A sensitivity test

The ability to find convex trade-offs between biodiversity and yield depends critically on differential impact on biodiversity and target species by gear or by space. We ran a sensitivity/demonstration of this by simplifying the California Current model to a single gear (bottom trawl), two target species (black cod and halibut), and a single bycatch species (VMEs). The abundance of each species was equal in all areas. In this case, there is a linear trade-off between the VME and target species catch. As more area is closed to trawling, there is less target species catch, but higher VME abundance.

Discussion

Can area-based management contribute to reducing global hunger while protecting biodiversity? These examples demonstrate that there is potential to maintain high levels of biodiversity without sacrificing much food production. The key feature of these examples is that important components of biodiversity are either spatially isolated and or differentially affected by various fishing gears. Both of these conditions are common to many fisheries. Vulnerable marine ecosystems and sensitive biota are typically spatially isolated and almost always sensitive to some gears, but not others. Sensitive benthic species, such as corals and sponges, are found in high density in relatively few locations, and are particularly vulnerable to mobile bottom-contact gear such as bottom trawls or dredges, are somewhat impacted by bottom longlining, but are generally unaffected by gear that does not touch the bottom. Marine birds are typically caught by longline gear, but not by purse seine, although in some cases, purse seining may reduce prey abundance or disperse fish aggregations reducing bird foraging efficiency (Tasker et al., 2000). Dive fisheries and hook-and-line fishing commonly have little direct impact on other species – thus some of the fisheries for tuna that are recommended by the Seafood Watch program of Monterey Bay Aquarium or have received MSC certification have generally been hook and line fisheries.

Detailed data are available for benthic ecosystems, and there is clear evidence that vulnerable biota are highly concentrated (Parker *et al.*, 2009), as is bottom-trawl fishing effort (Amoroso *et al.*, 2018). Bird species are particularly vulnerable near nesting sites (Cury *et al.*, 2011) and to longline gear (Melvin *et al.*, 2004). Different marine mammals are impacted by a range of fishing gears, with whale entanglement in pot gear and hooking on longline gear for smaller cetaceans perhaps the most common. Turtles are also impacted by longline gear.

When target species are found in a different area than biota of concern, then there are win-win solutions using spatially-explicit "mosaic closures" (Walters and Martell, 2004). However, modern fisheries management requires analysis of impacts on multiple species at the same time, and the differential impact of specific gears on species of concern provides further potential for win-win solutions.

These examples are illustrations and may have exaggerated the impact of fishing gears on non-target species. Thus in both cases, biodiversity in the revenue maximization case was very low. This may or may not be true of most real fisheries, but the critical element of these examples – that biodiversity can be protected by spatial and gear management – can be considered a hypothesis to be further explored.

These illustrative models omit a number of factors that can be important. We have not considered movement between areas or trophic impacts. In addition to regulation by space and gear, many fisheries have bycatch avoidance by temporal closures of area, and we have not considered modifications to fishing gear or fishing behavior that have been a major method used to reduced impact on non-target species of conservation interest. Finally, we have not considered the economics of fishing; we have only looked at revenue maximization.

The win-win solutions would likely be even better if fisheries profit was considered rather than revenue. Profit is typically maximized at a lower fishing effort

than yield (Grafton *et al.*, 2007), so there will be less biodiversity impact of a profit-maximizing solution than a revenue-maximizing solution.

We have shown that area- and gear-based effort regulations can provide for high levels of biodiversity and harvest. Perhaps most striking in these two examples is that notake areas do not prove optimal until almost all weight is placed on maximizing biodiversity. This is largely because in our two examples, there are fishing gears that had little or no impact on the key species of conservation concern, so those gears were still part of the optimal mix even when there was high weight on biodiversity maximization. Again, this is a hypothesis to be tested in any individual ecosystem.

When there is no separation of bycatch and target catch by area or gear, we demonstrated in the sensitivity run that the trade-off becomes linear. An important area for further research is to examine the empirical data on the spatial correlation of these factors.

This result runs contrary to the arguments that only no-take areas protect biodiversity adequately (Lubchenco and Grorud-Colvert, 2015). By definition, each of our modeled areas was a marine protected area, but true no-take areas were rarely an optimal outcome. Society may indeed want no-take areas as protection of historical sites, tourist destinations, and scientific reference areas, but it seems unlikely that no-take areas are necessary to protect biodiversity if gear and area-specific regulation of fishing effort can be implemented.

These examples provide evidence that well-implemented area-based fisheries management can achieve biodiversity protection and should be counted as "other effective area-based conservation measures" that contribute towards the Aichi and IUCN targets. The closure of the large portions of the Aleutian Islands to bottom trawling has protected much of the most sensitive benthic communities and streamer lines in longline fisheries have been much more effective at protecting marine birds than setting aside 30% of the area as a no-take area. To achieve the potential win-win solutions, several steps must be taken. First, the species of highest priority for protection need to be identified and their distributions mapped. Second, the threats different fishing gear pose to specific species need to be clearly defined. Modification to fishing gear or methods may be the most effective way to reduce a threat, but if the threat cannot be reduced by changing fishing practices, closing areas of high abundance of species of concern to the gear that impacts them needs to be implemented and enforced. While many countries currently lack effective enforcement, the growing availability of inexpensive vessel tracking devices should enable almost all countries to implement area closures for specific gears.

We have not examined several other specific approaches to area-based management that have shown effective reductions in fishing impact on species of concern and make win-win solutions even more likely. One approach is time—area closures, where certain areas are closed to specific gears at certain times of the year when species of concern are particularly vulnerable (Hoos *et al.*, 2019; Smith *et al.*, 2019). The second approach is real-time closures, where impact on specific biota is monitored in real time and hot spots of impact closed (Little *et al.*, 2014). Third are so-called "move on rules" in which vessels are required to leave an area if they reach specific bycatch targets (Cournane *et al.*, 2013; Dunn *et al.*, 2014). Finally, various jurisdictions have implemented bycatch quotas where individual vessels or fleets have a quota for catch of

species of concern and the vessel or fleet must cease fishing if it reaches the quota (Wallace *et al.*, 2015). This provides strong incentives for vessels to avoid areas where catch of species of concern is likely, but bycatch quotas and move-on rules do require atsea monitoring of the catch. These and other area-based management measures have the capacity to maintain high levels of biodiversity, while simultaneously allowing high levels of fishing revenue and provision of an important and sustainable global food source.

Data availability

The data underlying this article are available in the online Supplementary material.

Supplementary material

The following Supplementary material is available at *ICESJMS* online: Table S1 – values of the parameters for the BSAI gear types and areas, and Table S2 – values of the parameters for the California coast gear types and areas.

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Author contributions

RH was involved in the conceptualization of the study, formal analysis, investigation, development of methodology, project administration, procurement of resources, software, supervision, validation, and writing. CAA, HP, and GAW were involved in data curation, formal analysis, visualization, reviewing, and editing.

References

- Amoroso, R. O., Pitcher, C. R., Rijnsdorp, A. D., McConnaughey, R. A., Parma, A. M., Suuronen, P., Eigaard, O. R., *et al.* 2018. Bottom trawl fishing footprints on the world's continental shelves. Proceedings of the National Academy of Sciences, 115: E10275–E10282.
- Brown, C. J., and Mumby, P. J. 2014. Trade-offs between fisheries and the conservation of ecosystem function are defined by management strategy. Frontiers in Ecology and the Environment, 12: 324–329.
- Cournane, J. M., Kritzer, J. P., and Correia, S. J. 2013. Spatial and temporal patterns of anadromous alosine bycatch in the US Atlantic herring fishery. Fisheries Research, 141: 88–94.
- 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.

- Dunn, D. C., Boustany, A. M., Roberts, J. J., Brazer, E., Sanderson, M., Gardner, B., and Halpin, P. N. 2014. Empirical move-on rules to inform fishing strategies: a N ew E ngland case study. Fish and Fisheries, 15: 359–375.
- FAO. 2018. The State of World Fisheries and Aquaculture 2018 Meeting the sustainable development goals. Rome, Licence: CC BY-NC-SA 3.0 IGO.
- Garcia, S. M. 1994. The precautionary principle: its implications in capture fisheries management. Ocean and Coastal Management, 22: 99–125.
- Grafton, R. Q., Kompas, Q., and Hilborn, R. W. 2007. Economics of Overexploitation Revisited. Science, 318: 1601.
- Hilborn, R. 2011. Future directions in ecosystem based fisheries management: A personal perspective. Fisheries Research, 108: 235–239.
- Hoos, L. A., Buckel, J. A., Boyd, J. B., Loeffler, M. S., and Lee, L. M. 2019. Fisheries management in the face of uncertainty: Designing time-area closures that are effective under multiple spatial patterns of fishing effort displacement in an estuarine gill net fishery. PLoS ONE, 14(1):e0211103. doi: 10.1371/journal.pone.0211103.
- Little, A. S., Needle, C. L., Hilborn, R., Holland, D. S., and Marshall, C. T. 2014. Real-time spatial management approaches to reduce bycatch and discards: experiences from Europe and the United States. Fish and Fisheries, 16(4): 576–602.
- Lubchenco, J., and Grorud-Colvert, K. 2015. Making waves: The science and politics of ocean protection. Science, 350: 382–383.
- Melvin, E. F., Sullivan, B., Robertson, G., and Wienecke, B. 2004. A review of the effectiveness of streamer lines as a seabird by-catch mitigation technique in longline fisheries and CCAMLR streamer line requirements. CCAMLR Science, 11: 189–201.
- Parker, S. J., Penney, A. J., and Clark, M. R. 2009. Detection criteria for managing trawl impacts on vulnerable marine ecosystems in high seas fisheries of the South Pacific Ocean. Marine Ecology Progress Series, 397: 309–317.
- Rassweiler, A., Costello, C., Hilborn, R., and Siegel, D. A. 2014. Integrating scientific guidance into marine spatial planning. Proceedings of the Royal Society B-Biological Sciences, 281, https://doi.org/10.1098/rspb.2013.2252
- RCoreTeam 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rice, J., Garcia, S. M., and Kaiser, M. J. 2018. Other Effective Area-Based Conservation Measures (OEABCMs) Used in Marine Fisheries: A Working Paper. https://www.cbd.int/doc/c/0689/522e/7f94ced371fa41aeee6747e5/mcb-em-2018-01-inf-04-en.pdf
- Smith, J. A., Tommasi, D., Sweeney, J., Brodie, S., Welch, H., Hazen, E. L., Muhling, B., *et al.* 2019. Lost opportunity: Quantifying the dynamic economic impact of time-area fishery closures. Journal of Applied Ecology, 57(3): 502–513.
- Tasker, M. L., Camphuysen, C., Cooper, J., Garthe, S., Montevecchi, W. A., and Blaber, S. J. 2000. The impacts of fishing on marine birds. ICES Journal of Marine Science, 57: 531–547.

- Wallace, S., Turris, B., Driscoll, J., Bodtker, K., Mose, B., and Munro, G. 2015. Canada's Pacific groundfish trawl habitat agreement: A global first in an ecosystem approach to bottom trawl impacts. Marine Policy, 60: 240–248.
- Walters, C. J., and Martell, S. J. 2004. Fisheries Ecology and Management. Princeton University Press. 448 pp.
- White, C., Halpern, B. S., and Kappel, C. V. 2012. Ecosystem service tradeoff analysis reveals the value of marine spatial planning for multiple ocean uses. Proceedings of the National Academy of Sciences, 109: 4696–4701.
- Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., *et al.* 2009. Rebuilding Global Fisheries. Science, 325: 578–585.

Table 1. Definition of parameters used in equations 1–6.

Parameter	Definition
B_{sa}	Abundance of species <i>s</i> in area <i>a</i> (tons)
E_{ga}	Effort by gear g in area a
C_{sa}	Catch of species s in area a (tons)
r_s	Intrinsic rate of increase for species s
k_{sa}	Unfished stock size for species s in area a (tons)
u_{sa}	Exploitation rate for species s in area a
q_{gs}	Exploitation rate by one unit of effort of gear g on species s
R_{ga}	Revenue from gear g in area a (\$)
p_s	Price for species s (\$)
D	Total value of biodiversity
$\mathcal{V}_{\mathcal{S}}$	Relative biodiversity value of species s
V	Total value to be optimized
W	Proportion of total value assigned to revenue
Dmax	Maximum value of biodiversity
R_{max}	Maximum value of revenue (\$)

Figure Captions

- **Figure 1.** Spatial management in Alaska. Different colors or shades indicate different kinds of protection. In addition, effort and catch of species of fish and invertebrates are also allocated by area.
- **Figure 2.** The tradeoff between total abundance of fish and the sustainable harvest for a single species model (dashed line) and a multispecies ecosystem (Worm *et al.*, 2009) (solid line).
- **Figure 3.** Maps of the regions for the Bering Sea case study (a) and the California current (b).
- **Figure 4.** (a) The abundance of three species and total revenue for different weighting of biodiversity. (b) Trade-off between fishing revenue and biodiversity value for the Bering Sea and Aleutian Islands case study.
- **Figure 5.** (a) The abundance of three species and total revenue for different weighting for biodiversity. (b) Trade-off between fishing revenue and biodiversity value for the California Current case study.