



Original Article

What unmanaged fishing patterns reveal about optimal management: applied to the balanced harvesting debate

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Balanced harvesting (BH)—the idea of harvesting all species and sizes in proportion to their production rate—has been a topic of recent debate. Developed world fisheries tend to fish more selectively, concentrating on certain species and sizes preferred in the market. However, fishing patterns in some developing countries, with a range of different fishing gears and more generalist markets, more closely resemble BH. The BH debate therefore hinges on whether selective fisheries should become more balanced, whether unselective fisheries should do the opposite, both, or neither. In this study, we use simple and general analytical theory to describe the ideal free distribution that should emerge in unmanaged fisheries, and we show that this ideal free distribution should approximately produce BH only when prices, catchabilities, and fishing costs are similar across species and sizes. We then derive general properties of yield and profit maxima subject to conservation constraints. We find that BH is unlikely to be optimal in any fishery but may be closer to optimal in fisheries in which it emerges without management. Thus, BH may be more useful as a heuristic for understanding differences between fisheries in locally appropriate management than as an exact management strategy.

Keywords: balanced harvesting, bioeconomic model, ecosystem-based fisheries management, ideal free distribution, productivity

Introduction

Balanced harvesting (BH) has been a topic of recent controversy in fisheries science (Kolding *et al.*, 2016; Zhou *et al.*, 2019). BH calls for fishing a wide range of species and sizes of fish in an ecosystem in proportion to their natural productivity (Zhou *et al.*, 2010, 2014; Garcia *et al.*, 2012; Law *et al.*, 2016), in contrast to the common practice—especially in developed world fisheries—of fishing selectively on certain sizes and species, often disproportionately the larger ones (Garcia *et al.*, 2012). More precisely, there are at least two different definitions of BH, specifying that fishing mortality rate on each group (size and species) is proportional to: (i) its gross production rate, P , with dimensions mass per unit time or (ii) its productivity, i.e. production per unit biomass, P/B , with dimensions per unit time (Garcia *et al.*, 2012; Law *et al.*, 2016; Plank, 2016; Heath *et al.*, 2017). In this study, we

adopt definition (i), which has the advantage that, as a stock becomes depleted, its gross production and therefore its specified fishing mortality decrease (Heath *et al.*, 2017). This is similar to a “state-dependent” or “sliding” harvest control rule for target species (Berger *et al.*, 2012). It is likely to be more difficult to implement than definition (ii), as it requires up-to-date information on stock biomass (Zhou *et al.*, 2019). However, its explicit protection of depleted stocks fulfils BH’s aim of maintaining the species richness of marine ecosystems (Heath *et al.*, 2017).

Proposals for BH have argued that harvesting more species and shifting harvest towards smaller, more productive sizes can increase the fishery yields substantially (Garcia *et al.*, 2012; Zhou *et al.*, 2015) and that the BH pattern maintains the relative abundances of different sizes and species (Law *et al.*, 2015, 2016; Kolding *et al.*, 2016a), even though overall fish biomass is reduced

(e.g. Kolding and van Zwieten, 2014). They argue that BH therefore offers a path to meeting food production requirements while minimizing impact on ecosystem structure, which are key international fishery management objectives (Garcia *et al.*, 2016).

Criticisms of BH have argued that harvesting small sizes and currently unfished species could have significant economic costs (Burgess *et al.*, 2016), that fishing juvenile sizes would be detrimental to yields, that models that suggest otherwise are based on unrealistic assumptions [but this claim about model assumptions is disputed by Andersen *et al.* (2016)] (Froese *et al.*, 2016), and that other ecosystem objectives besides size structure would be harmed (Froese *et al.*, 2016), undermining BH's alignment with international management objectives (Pauly *et al.*, 2016). The BH debate also forms part of a broader debate about whether fisheries targeting forage fish should become larger, to support more food production (e.g. Kolding *et al.*, 2016b), or smaller to support higher yields in more economically valuable predator fisheries (e.g. Smith *et al.*, 2011).

One factor, which may be partly at the root of both of these debates, is the fact that fishing patterns and objectives differ substantially across regions of the world. Costello (2017) describes two contrasting archetypal patterns, which he calls "World A" and "World B", that provide a useful frame for considering BH (though this frame is of course heuristic, and most fisheries fall somewhere along a spectrum between these archetypes; see, e.g. Kolding *et al.*, 2016c). In World A, in which Costello (2017) includes much of Europe, North America, Australia and New Zealand, fishing is selectively concentrated on a relatively small set of sizes and species and most fish stocks are managed using some form of single-species management based on the principle of maximum sustainable yield (MSY) (Skern-Mauritzen *et al.*, 2016). In World B, in which Costello (2017) includes much of Asia and perhaps other developing countries, consumers value a wider range of species and sizes, and fishing gears and strategies are consequently less selective. As a result, fishing pressure ends up being more balanced relative to productivity (e.g. Kolding and van Zwieten, 2014), although managed BH would aim to avoid the disproportionate depletion of large predator species observed by Szuwalski *et al.* (2017) in the East China Sea. There is often comparatively lighter management in World B than in World A, and what management there is less oriented around MSY, and arguably less oriented around strictly profit objectives (e.g. Cao *et al.*, 2017). Overall yields tend to be higher in World B than in World A but dominated by small fish, at the expense of removing predators and thereby releasing smaller forage species from predation mortality (Jacobsen *et al.*, 2014; McCann *et al.*, 2016; Andersen and Gislason, 2017; Szuwalski *et al.*, 2017).

Using Costello's (2017) frame, if there were a one-size-fits-all approach to ecosystem-based fisheries management (EBFM), would it involve fishing patterns looking more like World B (more balanced), as some BH proposals seem to suggest (e.g. Zhou *et al.*, 2015), or would it look more like World A (less balanced), as some criticisms seem to suggest (e.g. Froese *et al.*, 2016)? If there was not a one-size-fits-all approach, what would ideal management patterns look like in each world? From the perspective of the BH debate, the key question is whether fisheries currently fishing in relatively balanced patterns would benefit from switching to more selective patterns, whether fisheries currently fishing in relatively selective patterns would benefit from switching to more balanced patterns, both, or neither. A more general version of this question is: what does a fishery's

unmanaged fishing pattern tell us about what its ideally managed fishing pattern would look like?

In this study, we use a simple and general analytical theory to demonstrate how differences in price, catchability, fishing cost, and productivity across different ecosystem components (e.g. species or body size classes) determine their relative exploitation rates in an unmanaged fishery. This theory distills, generalizes, and expands on our recent theories addressing this question in more complex models (Burgess, 2015; Plank, 2016; Plank *et al.*, 2017; Hackney *et al.*, 2019). From this, we argue that large differences in prices, catchabilities, and costs across sizes and species in World A, as compared to those in World B, are key to explaining the contrasting fishing patterns in these different ecosystems described above. To explore the consequences of these differences for management prescriptions, we then derive general properties of yield maxima and profit maxima subject to conservation constraints, all at the ecosystem-level, as a rough proxy for different possible EBFM objectives. We illustrate these properties in a simple predator-prey model (Figure 1) and analyse the general case in Appendix A. We discuss what insights observations of fishing patterns in lightly managed systems might provide for designing management in those systems, in general and in the context of the BH debate specifically.

Materials and methods

We consider an ecosystem comprised of N groups: these could represent species, functional groups, or within-species age or size classes. Group i has biomass B_i (\mathbf{B} is the vector of biomasses of all groups), surplus production rate S_i (units of mass per unit time; equal to production due to growth and recruitment, minus biomass lost due to natural mortality and metabolic expenditure) and fishing mortality rate F_i (per unit time). Surplus production S_i may be influenced by the biomass of one or more groups via predator-prey or competitive interactions among species; or demographic relationships between sizes. However, we do not specify a particular model for these interactions and leave the model in a general form. The rate of change of group i 's biomass is thus given by

$$\frac{dB_i}{dt} = S_i(\mathbf{B}) - B_i F_i. \quad (1)$$

We assume that there are a fixed number of fishing agents: these could represent individual fishers, small collectives, or large commercial organizations. Each agent can choose how to allocate their fishing effort among the N groups. The aggregate fishing mortality for group i is

$$F_i = q_i E_i, \quad (2)$$

where q_i is the catchability of group i and E_i is the total fishing effort applied to group i summed over all agents. The yield from group i is

$$Y_i = q_i E_i B_i. \quad (3)$$

The total profit obtained from fishing group i is

$$\pi_i = p_i q_i E_i B_i - c_i E_i, \quad (4)$$

where p_i is the market price per unit mass (minus the processing/handling cost per unit mass) and c_i is the cost per unit effort on

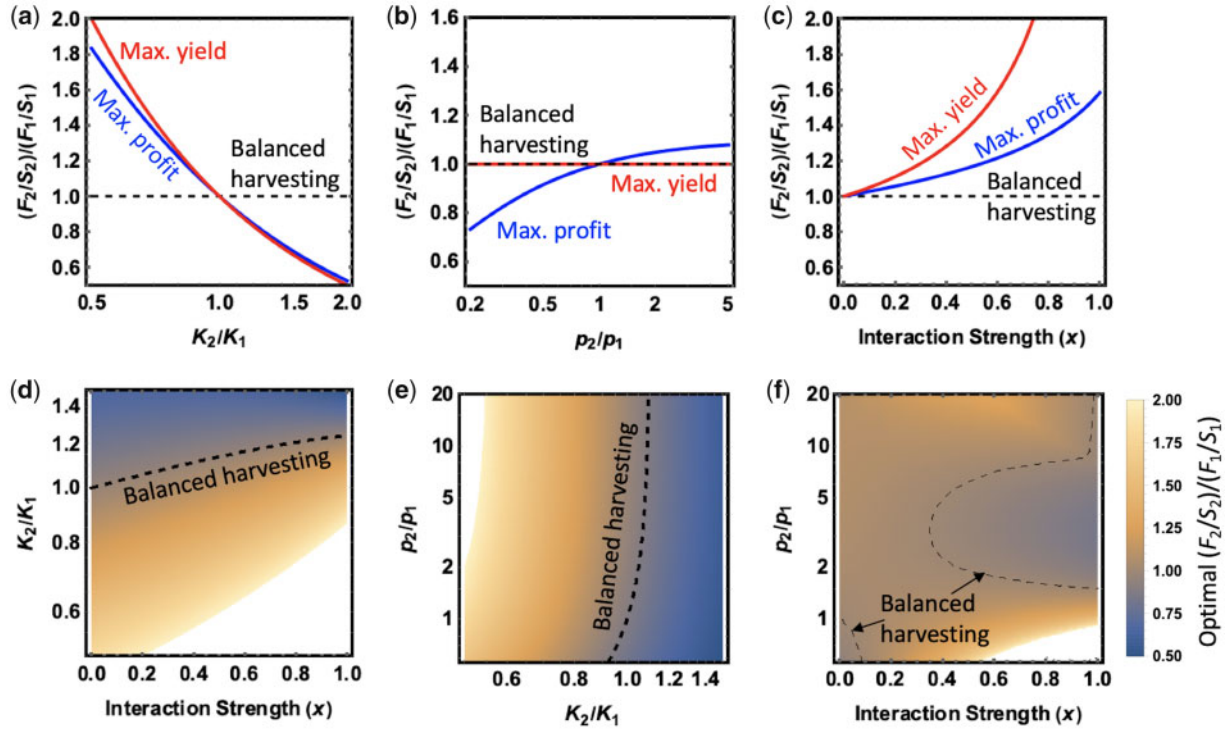


Figure 1. Effects of (a) carrying capacity (K_i), (b) price (p_i), (c) interaction strength (x), (d) carrying capacity combined with interaction strength, (e) price combined with carrying capacity, and (f) price combined with interaction strength, on the profit-maximizing (all panels) and yield-maximizing (shown in a–c) fishing patterns, relative to BH. Optimal fishing pattern (red and blue lines in a–c; colours in d–f; comparing fishing mortality rates, F_i , to surplus production, S_i) is shown as a function of the variable(s) indicated. Assuming that production (P_i) is proportional to surplus production (S_i), BH occurs when $F_1/S_1 = F_2/S_2$ (black dashed lines). All panels use the model described by (16)–(19). Default parameter values are: $r_1 = 1$, $r_2 = 0.5$, $K_1 = K_2 = p_1 = p_2 = 1$, $q_1 = q_2 = 0.1$, $c_1 = c_2 = 0.01$, $e = 0.1$, $x = 0$. In each panel, parameter values are varied from these defaults as indicated on the x-axis in (a)–(c), and on the x- and y-axes in (d)–(f). Colour bars in (d)–(f) are truncated at 2 [i.e. white indicates $(F_2/S_2) > 2(F_1/S_1)$].

group i . The marginal profit (i.e. the derivative of profit with respect to effort) from group i , denoted π_{Ei} is, therefore,

$$\pi_{Ei} = p_i q_i B_i - c_i. \quad (5)$$

Results

Ideal free distribution

The ideal free distribution of the fishing agents is achieved when the marginal profit π_{Ei} is the same, say π_E^* , for all harvested groups (that is all groups for which $E_i > 0$). Intuitively, this corresponds to a Nash equilibrium of the decision problem faced by the fishing agents because it means that no agent can increase their profit by reallocating their effort among the N groups. The parameter π_E^* can be thought of as the threshold profit required to induce agents to fish. High levels of π_E^* correspond to low levels of harvesting, as only the most profitable groups will be economically viable to harvest. Lower levels of π_E^* correspond to higher levels of harvesting and *vice versa*. Unmanaged bioeconomic equilibrium occurs where there is zero profit (Clark, 1976), if fleet-wide effort is constrained only by economic opportunity (i.e. open access). In our model, this implies that $\pi_E^* = 0$ (zero profit implies zero marginal profit because our model assumes that profit is linear in effort). If fleet-wide effort was constrained by something other than economic opportunity

(e.g. available boats, permits, or workforce), profits at the unmanaged equilibrium could be positive, but fishing effort would still be distributed according to the ideal free distribution. However, regulations or other factors that prevent fishers from freely switching fisheries could prevent the ideal free distribution from occurring; thus, our analysis only assumes that the ideal free distribution occurs in unmanaged or lightly managed contexts.

At any bioeconomic equilibrium, where the ideal free distribution is realized and where biomass is not changing in any group (i.e. $\frac{dB_i}{dt} = 0$ for all i):

$$p_i q_i \frac{S_i}{F_i} - c_i = \pi_E^*, \quad (6)$$

for all harvested groups. Hence, for each group (regardless of the functional forms of $S_i(\mathbf{B})$ for each i), either

$$F_i = \left(\frac{p_i q_i}{c_i + \pi_E^*} \right) S_i \text{ (harvested groups),} \quad (7a)$$

or

$$p_i q_i B_i - c_i < \pi_E^*, \text{ and } F_i = 0 \text{ (unharvested groups).} \quad (7b)$$

From (7a), we can see that, if all ecological groups are harvested with the same catchability (i.e. same q_i for all i) and same

cost (c_i) and receive the same price (p_i), then fishing agents' ideal free distribution will eventually result in fishing mortality being proportional to surplus production ($F_i \propto S_i$ with the same proportionality constant for all i), and equal biomass across harvested groups [because $B_i = S_i/F_i$ at equilibrium, from (1)]. Plank (2016), Plank *et al.* (2017), and Hackney *et al.* (2019) find this result numerically in three different ecosystem models. However, if there are differences among ecological groups in q_{ij} , c_j , or p_i , then $F_i \propto S_i$ will not generally be the equilibrium outcome, unless these differences exactly cancel out such that $\frac{p_i q_{ij}}{c_j + \pi_E}$ has the same value for all i .

While our model has so far made the unrealistic assumption that fishing agents can perfectly select among groups when they fish (i.e. they catch one species and size at a time, with no bycatch), our insight—that $F_i \propto S_i$ naturally emerges if prices, costs, and catchabilities are similar across ecological groups—is more general. For instance, suppose now that fishing agents choose to target fishing opportunities (Branch *et al.*, 2005; also called “métiers”, ICES, 2003; Reid *et al.*, 2016) instead of individual ecological groups, and fishing opportunity j results in per-unit-effort catches of group i of $q_{ij}B_i$ and cost c_j . The marginal profit from fishing opportunity j is

$$\pi_{Ej} = \sum_i p_i q_{ij} B_i - c_j. \quad (8)$$

Suppose further, following Burgess (2015), that q_{ij} can be broken down into two components, $q_{ij} = a_i m_{ij}$, where a_i measures how easy group i is to catch relative to other groups and m_{ij} measures which groups fishing opportunity j targets relative to other groups and has the property that $\sum_i m_{ij} = 1$, for all j . Equation (8) then becomes

$$\pi_{Ej} = \sum_i p_i a_i m_{ij} B_i - c_j. \quad (9)$$

If all ecological groups are equally easy to catch ($a_i = a$, for all i) and have the same price ($p_i = p$, for all i) and effort in all fishing opportunities has the same cost ($c_j = c$, for all j , which implies that some groups are not cheaper than others to target), then (9) becomes

$$\pi_{Ej} = pa \sum_i m_{ij} B_i - c. \quad (10)$$

Under these conditions, all possible fishing opportunities will have equal marginal profit if all ecological groups have equal biomass (i.e. $B_i = B$ for all i). If ecological groups do not have equal biomass, then fishing opportunities that disproportionately target groups with higher biomass will have higher marginal profit and thus will attract greater effort and eventually lower the biomass of those groups. As a result, the ideal free distribution of fishing across fishing opportunities under these conditions will eventually result in the biomasses of all ecological groups being equal, unless there are no fishing technologies available allowing more abundant groups to be disproportionately targeted and any groups having smaller biomass are already not being fished at all (i.e. $m_{ij} = 0$, for all j , for such a group i) [see Burgess (2015) for proof of these results in a very similar model].

If ecological groups are not equally easy to catch and fetch different prices, or fishing opportunities have different costs (a_i , p_i , and c_j differ across i , j), then—by the same logic as above—the ideal free distribution will result in biomasses of all harvested

groups approaching (11) at any biological equilibrium, as the diversity of available fishing technologies increases [see equation (8) in Burgess (2015), and surrounding discussion]:

$$B_i = \frac{\pi_E^* + c_{\min}}{p_i a_i}, \quad (11)$$

where c_{\min} denotes the cheapest per-unit-effort cost among available fishing technologies. Equation (11) implies (because $B_i = S_i/F_i$ at equilibrium)

$$F_i = \left(\frac{p_i a_i}{\pi_E^* + c_{\min}} \right) S_i. \quad (12)$$

From (12), which mirrors (7a), we can see that $F_i \propto S_i$ occurs if p_i and a_i are the same across ecological groups, or if the differences cancel out in their effects on $\frac{p_i a_i}{\pi_E^* + c_{\min}}$.

Relation to BH

Under the definition of BH we adopt, fishing mortality rate is proportional to the gross production rate (with dimensions mass per unit time), denoted P_i for group i (Law *et al.*, 2016; Heath *et al.*, 2017; Zhou *et al.*, 2019). The above analysis shows that, when prices, costs and catchabilities are similar across groups, biomasses B_i are equalized across exploited groups and the fishing mortality F_i that emerges is proportional to the surplus production rate S_i of each group. Surplus production rate is given by

$$S_i = P_i - M_i B_i, \quad (13)$$

i.e. production net of losses due to natural mortality with rate $M_i B_i$ (per unit time). There is evidence that production rate P_i and natural mortality rate M_i are negatively correlated with trophic level (see, e.g. Kolding *et al.*, 2016b), and hence positively correlated with each other. Hence, if F_i is proportional to S_i , we would expect F_i to be approximately proportional to P_i in other words BH. The result of equal biomass across groups in our model has some parallels to the Sheldon size spectrum produced by BH in size-spectrum models (e.g. Law *et al.*, 2016), though may not be completely realistic at the level of sizes by species (see, e.g. Trebilco *et al.*, 2013). In contrast, when prices, costs, and/or catchabilities differ across groups, BH will not be the equilibrium outcome. The larger the differences $p_i q_{ij}/c_j$ across groups, the less the equilibrium harvesting pattern will resemble BH. More specifically [see (7a) and (12)], groups with higher prices and catchabilities, and lower costs, will be fished disproportionately hard, and *vice versa*. Moreover, groups without markets (i.e. $p_i = 0$) will not be fished at all, unless they are caught as bycatch in unselective gears.

Implications for optimized management

In the previous section, we showed analytically that approximate or partial BH should emerge from fishing agents' ideal free distribution in fisheries where costs, prices (per unit biomass), and catchabilities were similar across ecological groups (species, sizes, or functional groups) and where there were no technological constraints severely limiting how heavily groups could be targeted relative to one another. In fisheries where any of these conditions was violated, we would not expect to see BH emerge without some form of management intervention. Thus, observing

BH or not observing BH in an unmanaged fishery implicitly tells us something about prices, costs, catchabilities, and technologies. Below, we briefly consider what the management implications of this information might be, especially in the context of how suited BH might be to achieving various common management objectives. Future research could use a similar analysis to evaluate other possible fishing strategies besides BH.

For this analysis of management implications, we consider two possible management objectives: (i) maximize ecosystem-wide fishing profits, subject to conservation constraints, and (ii) maximize ecosystem-wide fishing yields, subject to conservation constraints. There are of course many other possible fishery management objectives, but these are representative of many objective sets discussed in the BH debate.

We also make three simplifying assumptions to make our analysis tractable. First, we assume that managers do not discount future yields or profits. This assumption reduces the manager's optimization exercise to a simple optimization of equilibrium yields or profits, rather than requiring dynamic optimization, because no discounting ensures that the dynamically optimal fishing path for a given set of objectives would eventually result in the equilibrium optimum for that same objective set. Second, we assume that there is either enough selectivity or enough fleet diversity (see Burgess 2015) that the manager's optimization exercise uses the group-specific harvesting model, described by (3) and (4) and the paragraph preceding them. Third, we assume that it is possible to define a differentiable mapping from efforts targeting each group ($E \equiv \{E_1, \dots, E_N\}$) to equilibrium biomasses (or average biomasses, if there is cycling around the equilibrium) of all groups, B . This mapping (for equilibrium biomasses) would be defined by setting the right-hand side of (1) equal to zero for all groups simultaneously and solving the resulting system of equations. However, despite these assumptions, we will derive qualitative insights that should generalize to more complex models.

Suppose that the conservation constraints imposed by the manager are lower-limit constraints on the biomass of each ecological group— L_i denotes the constraint for group i . If group i is not targeted for protection by management, then $L_i = 0$, because an ecological group cannot physically have negative biomass. We denote the vector of conservation constraints L ($L = \{L_1, \dots, L_N\}$). In choosing the optimal fishing efforts, E , there is the additional constraint that all efforts must be non-negative. Thus, the managers' optimization problem is given by (14) if the objective is yield maximization and (15) if the objective is profit maximization:

$$\max_E \sum_i q_i E_i B_i(E) \quad \text{subject to: } B_i(E) \geq L_i, \text{ and } E_i \geq 0, \text{ for all } i, \quad (14)$$

$$\max_E \sum_i (p_i q_i E_i B_i(E) - c_i E_i) \quad \text{subject to: } B_i(E) \geq L_i, \text{ and } E_i \geq 0, \text{ for all } i. \quad (15)$$

We explore this optimization problem, in relation to BH, in a simple two-species illustrative example below and in Figure 1. We analyse the general case in Appendix A.

In our illustrative example, there are two harvested species, which are prey (sp. 1) and predator (sp. 2). The growth of each is logistic, with an added interaction term, implying that the predator is not a specialist on this particular prey and has other sources

of prey that are assumed to be fixed. This allows us to vary the ecological interaction strength—to examine its importance to the unmanaged and optimally managed outcomes—without making the predator unviable. The two species grow according to:

$$\frac{dB_1}{dt} = B_1 \left(r_1 \left[1 - \frac{B_1}{K_1} \right] - x B_2 - q_1 E_1 \right), \quad (16)$$

$$\frac{dB_2}{dt} = B_2 \left(r_2 \left[1 - \frac{B_2}{K_2} \right] + e x B_1 - q_2 E_2 \right). \quad (17)$$

Here, x is the predator–prey interaction rate, and e is the efficiency of biomass conversion from prey to predators. Surplus production (S_i) is given by:

$$S_1 = B_1 \left(r_1 \left[1 - \frac{B_1}{K_1} \right] - x B_2 \right), \quad (18)$$

$$S_2 = B_2 \left(r_2 \left[1 - \frac{B_2}{K_2} \right] + e x B_1 \right). \quad (19)$$

Equilibrium biomasses $\{B_1, B_2\}$, given efforts $\{E_1, E_2\}$, are found by setting $S_i = q_i E_i B_i$ for $i = 1, 2$, where S_i is given by (18) and (19), and solving for B_1 and B_2 . This is analytically tractable but produces an expression too complex to be insightful on visual inspection. Yields and profits are given by (3) and (4) for each species, and fishery-wide yields and profits are then given by the sum of species-specific yields and profits. Assuming unmanaged fishing efforts follow the ideal free distribution, and $S_i \propto P_i$ (which we assume hereafter), unmanaged efforts follow (7a, b), and the basic results about BH (i.e. $F_i \propto S_i \propto P_i$) without management discussed above apply (i.e. BH occurs at equilibrium if $p_1 q_1 = p_2 q_2$, and $c_1 = c_2$, but generally not otherwise).

When the two species do not interact (i.e. $x = 0$), yield is maximized by harvesting each at $F_i = r_i/2$, resulting in $B_i = K_i/2$, and $S_i = r_i K_i/4$ [the classic Schaefer (1954) MSY result]; and profit is maximized at $F_i = \frac{r_i}{2} \left(1 - \frac{c_i}{p_i q_i K_i} \right)$ (if $\frac{c_i}{p_i q_i K_i} < 1$; $F_i = 0$ otherwise), resulting in $B_i = \frac{1}{2} \left(K_i + \frac{c_i}{p_i q_i} \right)$ and $S_i = \frac{r_i}{4} \left(1 - \frac{c_i}{p_i q_i K_i} \right) \left(K_i + \frac{c_i}{p_i q_i} \right)$. The yield optimum is BH ($F_i \propto S_i$) if and only if $K_1 = K_2$. The profit optimum is BH if and only if $\left(K_1 + \frac{c_1}{p_1 q_1} \right) = \left(K_2 + \frac{c_2}{p_2 q_2} \right)$. Differences in carrying capacity (K_i) among the species move both yield and profit optima away from BH, towards proportionally heavier exploitation (higher F_i/S_i) on species with smaller carrying capacity (Figure 1a). Differences in catchability, price, and cost ($p_i q_i/c_i$) (the defining feature of World A, compared to World B) move profit optima away from BH, towards proportionally heavier exploitation on species with higher value (i.e. higher $p_i q_i/c_i$), though this effect is relatively weak (Figure 1b), and gets weaker the smaller $\frac{c_i}{p_i q_i K_i}$ terms are (i.e. the more profitable fishing is generally).

When the species do interact ($x > 0$), the predator (sp. 2) becomes disproportionately heavily exploited, relative to BH, as the strength of interaction (x) increases, under both yield maximization and profit maximization, if trophic transfers are inefficient (i.e. $e \ll 1$) and the predator grows more slowly than the prey ($r_2 < r_1$) (both realistic assumptions), all else (K_i, q_i, p_i, c_i) being equal (Figure 1c). The fact that prey species tend to have

higher carrying capacities than predators (e.g. Trebilco *et al.*, 2013) would make harvesting even more disproportionate on predators at unconstrained yield or profit maxima (Figure 1d). An important caveat to this result is that, due to the very large size differences between larval and adult life stages, fish communities are not well described by a food web of predator–prey interactions at species level (Jennings *et al.*, 2001). Many species typically thought of as high trophic level predators still act as a source of prey for species with smaller adult body mass.

The combined effect of predation rate ($x > 0$) and differences in carrying capacity (Figure 1d), and of differences in carrying capacity and price (or cost) (Figure 1e), on optimal fishing patterns, are intuitive. Optimal fishing mortality is greater than BH would prescribe on species with relatively low carrying capacity, high price (or low cost), and on the predator. However, the interaction between differences in price (or cost) and predation rate ($x > 0$), on optimal fishing pattern, is somewhat more complex (Figure 1f). When the prey is more valuable (higher price and/or lower cost), it can be optimal to cull the predator (i.e. harvest it to extinction) to maximize the value of the prey harvest (provided culling the predator is not prohibitively expensive). Conversely, when the predator is much more valuable than the prey, it is optimal to not harvest the prey at all, to preserve it for feeding the more valuable predator. In both of these cases, the predator is harvested more heavily, relative to the prey, than BH would prescribe. However, there are intermediate cases—when the predator is slightly more valuable than the prey—where the prey ends up being harvested slightly harder than the predator, relative to their respective surplus productions (S_i), than BH (region to the right of the dashed line in Figure 1f). This seems counterintuitive but occurs as a result of the predator population being maintained at a relatively high abundance—to facilitate its profitability for the fishery—which in turn reduces the prey's surplus production (which is the denominator in F_i/S_i) via the predation. Given that prices tend to positively correlate with body size and trophic level (e.g. Tsikliras and Polymeros, 2014), the cases in which the predator is more valuable than the prey are more relevant to real-world fisheries.

Moving from the example model of Figure 1 to the general case (see Appendix A), we find the following. First, BH is not the exactly optimal fishing pattern except under extremely restrictive and unrealistic conditions, in which ecological groups are either ecologically and economically identical, or the effects of their differences exactly counteract one other (see dashed line in Figure 1f for an example of this).

Second, ecosystems with fishery characteristics resembling World B (i.e. more similar price, catchability, and cost across species and sizes) should typically (but not necessarily always) have optimal fishing patterns that more closely resemble BH than ecosystems with fishery characteristics more closely resembling World A. One reason is that selective markets (i.e. markets where only a subset of species and sizes is marketable) restrict which ecological groups are harvested in the optimal pattern, similarly to the pattern that emerges under open access. For a non-marketable group to be harvested under the profit-maximizing pattern, its harvest would have to have a large enough indirect benefit on the profitability of a marketable group to offset the harvesting cost. A second reason may be that ecological and economic differences between ecological groups could often (albeit not always) move the optimal fishing pattern away from BH in similar directions (e.g. Figure 1e); and there are fewer economic

differences between ecological groups in World B than in World A, due to the former's more generalist markets and gears. Ecological differences promote greater fishing (relative to production) on groups that suppress other groups (predators) and that have low carrying capacity (e.g. Figure 1a and c). Economic differences promote greater fishing (relative to production) on groups with high price and catchability and low cost (Figure 1b). Predators tend to have higher prices (Tsikliras and Polymeros, 2014), and abundant species (with high carrying capacity) also tend to have lower prices (e.g. Courchamp *et al.*, 2006).

For these same reasons, we might naively expect yield objectives to produce optimal patterns that more closely resemble BH than profit objectives would (because yield objectives make economic differences between ecological groups irrelevant, and ecological and economic differences typically move the optimal fishing patterns away from BH in the same directions). However, fishing costs can make profit maximization more closely resemble BH than yield maximization (e.g. Figure 1a, c and f). Fishing costs limit the intensity with which species are optimally harvested generally (e.g. effort for maximum economic yield is lower than for MSY). High fishing costs and prices for predators relative to prey also reduce the benefits of culling predators to facilitate prey, which is often necessary to maximize yields (Matsuda and Abrams, 2006).

Third, conservation constraints should typically result in fishing patterns more similar to BH than the unconstrained cases. The reason is that conservation constraints only affect fishing patterns if they bind (e.g. if $B_i < L_i$ for group i , at the unconstrained optimum). If a conservation constraint binds for group i , it results in a lower F_i/S_i (because $B_i = S_i/F_i$ at equilibrium) than in the unconstrained optimum. Thus, for conservation constraints to move the optimal fishing pattern further away from BH than the unconstrained optimum, the constraints would have to disproportionately target, and bind for, ecological groups that were already more lightly fished (relative to production) than other groups not targeted by constraints. This seems unlikely. Cases where constraints bind for ecological groups that are relatively heavily fished seem more likely—and such constraints would move the optimal pattern towards BH.

Discussion

There is currently a debate as to whether fisheries should transition towards BH—harvesting all species and sizes in proportion to their production rate (Heath *et al.*, 2017)—to enhance fishery yields (and therefore food production) while meeting fisheries' biological objectives (Kolding *et al.*, 2016c). BH was originally defined as fishing mortality proportional to productivity, i.e. production per unit biomass, with dimensions per unit time (Garcia *et al.*, 2012). However, some subsequent studies have argued that fishing mortality should be proportional to gross production, with dimensions mass per unit time, as a means of protecting rare or depleted ecosystem components (Law *et al.*, 2016; Plank, 2016; Heath *et al.*, 2017). This is the definition we adopted in this study, although the alternative approaches are the subject of ongoing research (Zhou *et al.*, 2019).

Two of the major criticisms of BH are that it is likely to be economically costly, at least at a global scale (Burgess *et al.*, 2016), and that it may be technologically challenging (Burgess *et al.*, 2016; Froese *et al.*, 2016; Reid *et al.*, 2016), if not infeasible. Plank (2016), Plank *et al.* (2017), and Hackney *et al.* (2019) showed, in two different types of fishery models, that it is possible for BH to

emerge in unmanaged fisheries as a result of the rational choices fishers make. Kolding and van Zwieten (2014) found empirical evidence of this phenomenon in small-scale fisheries in African Lakes, where there is an absence of effective regulations on fishing selectivity. A somewhat similar pattern (albeit not BH) was found in the East China Sea, although this was characterized by indiscriminate fishing and depletion of high trophic level species (Szuwalski *et al.*, 2017), which managed BH would explicitly aim to avoid. These studies raised the possibility that BH may in some cases be feasible (because it seems to be occurring in some places) and raised the question of whether it was indeed in the economic interests of some fisheries (given that it seems to be in some places resulting from fisher decisions, which are presumed to be rational).

We used simple analytical theory to predict, in a general manner, if/when we would expect BH to emerge from rational fisher decision-making in an unmanaged context, and if/when we would expect BH to be a yield-maximizing or profit-maximizing fishing pattern subject to conservation constraints.

Our theory suggests that BH can indeed emerge in unmanaged fisheries, but only if different sizes, species, or functional groups have highly similar values (i.e. they have similar prices per unit biomass, costs, and catchabilities). Otherwise, unmanaged fishing will disproportionately concentrate on higher-value species and sizes. Fishers that target biomass yields, instead of profits, as an objective are more likely to fish according to BH in an unmanaged setting, because this objective makes all species' prices and costs effectively equal. Similarly, fishers that fish using highly unselective, indiscriminate gears (e.g. mosquito nets, bottom trawls) may be more likely to fish according to BH in an unmanaged setting, because these gears may have the tendency to equalize costs and catchabilities across species and sizes. These predictions seem to roughly match empirical reality: those fisheries in which patterns more closely resemble BH seem to be those with a wide range of gears and markets [i.e. Costello's (2017) "World B", including many small-scale and developing world fisheries, e.g. Kolding and van Zwieten 2014; Szuwalski *et al.*, 2017] and those fisheries in which markets and gears are more selective seem to have fishing patterns quite different from BH [Costello's (2017) "World A"].

Our theory suggests that BH is not likely to be the optimal fishing pattern (when maximizing yields or profits subject to conservation constraints) in any fishery, unless conservation constraints are binding in such a way as to prescribe BH (in our model, this would occur if all species and sizes were required by the manager to have the same equilibrium biomass). However, our theory suggests that optimal fishing patterns should in general more closely resemble BH in World B than in World A, especially when the objective is profits. Exceptions to this qualitative prediction could occur if incentives to deviate from BH because of value (price, cost, catchability), and incentives to deviate from BH because of ecology, worked in opposite directions (e.g. see the right-side BH region of Figure 1f). However, as we argued in the previous section (see also Figure 1 and Appendix A), such scenarios are more likely to be the exception than the rule.

Our theory does not offer clear general predictions regarding how severely sub-optimal BH would be with respect to yields or profits, though there may be reasons to hypothesize that BH would be substantially sub-optimal with respect to profits in many ecosystems, due to the requirement of harvesting unmarketable or marginally marketable sizes and species. For instance,

using a simple back-of-the envelope calculation, Burgess *et al.* (2016) projected that BH at a global scale might result in the fishing industry losing money on the aggregate, which would certainly be far from profit maximizing. The problem of unmarketable species would not affect BH's performance with respect to yield maximizing, and thus, BH may be closer to optimal with respect to yields. On the other hand, in cases where yield maximizing requires predator removal, BH could result in substantially lower yields (as would single-species MSY management; see, e.g. Szuwalski *et al.*, 2017). Among the management objectives considered in this study, we hypothesize that yield-maximizing subject to strict conservation constraints would produce the fishing patterns most closely resembling BH.

While we designed our theoretical framework to be as general as possible, it still required some assumptions. First and foremost, we assumed that surplus production (S_i) is proportional to gross production (P_i) and thus evaluated BH as fishing mortality proportional to surplus production. This assumption is likely to be violated to an extent so as to invalidate some of the very specific predictions of our model. For example, it is unlikely that equilibrium biomass will be exactly identical across species and sizes under BH. Size-spectrum models predict that this is not exactly the case, despite parallels to the Sheldon spectrum (Law *et al.*, 2016), and Kolding and van Zwieten (2014) found this not to be the case in Lake Kariba. Nevertheless, the empirical support for our broader qualitative predictions suggests that these are likely to be more robust. In particular, our theory predicts that BH is more likely to emerge in an unmanaged setting when prices, costs, and catchabilities are similar across species and sizes and is likely to be closer to optimal in World B than in World A, but not exactly optimal in either world.

Second, our theory predicting when BH would emerge in unmanaged fisheries assumed either perfect selectivity across sizes and species or an unrestricted range of fishing opportunity-specific catch mixes and very high diversity of fishing opportunities across this range (see Burgess, 2015). Neither of these assumptions is likely to be met exactly. As a consequence, BH is unlikely to exactly emerge in reality, even in unmanaged fisheries in which all sizes and species had equal value. However, our theory nonetheless provides a valid prediction: approximately equal prices, costs, and catchabilities (e.g. due to indiscriminate gears and markets), with a relatively wide range of possible catch mixes (e.g. due to a range of fishing habitats, times), will approximately result in BH. As discussed above, these approximate predictions have been observed empirically in some fisheries.

Third, we assumed a unique mapping from efforts to equilibrium biomasses (or average biomasses) and ignored changes in the stability of ecosystems and catches as either an outcome or a concern of fishery management. This is an important topic (e.g. see Anderson *et al.*, 2008; Essington *et al.*, 2015), but one we leave to future research. We also assumed bioeconomic equilibrium and ignored transient dynamics, which are known to be important in many biological and economic systems (e.g. Lande *et al.*, 2003; Sumaila *et al.*, 2012; Costello *et al.*, 2016). Of course, we cannot be sure that a stable equilibrium, or a representative set of temporal average abundances (in a cyclical or chaotic system), exists in the general case. In unmanaged fisheries, the industry's ability to adaptively switch between different species—to target those that are most abundant—could have a stabilizing effect on the targeted food webs, for analogous reasons to those that make generalist predators a stabilizing influence in food webs (McCann

and Rooney 2009). Under yield- or profit-maximizing management, the yield and profit benefits of exploiting relatively abundant species—all else equal—might also increase the targeted food web's stability. However, there also could be exceptions to this—for instance, cases where rarity-driven price increases or range contractions increase the profitability of harvesting rare ecological groups (Courchamp *et al.*, 2006; Burgess *et al.*, 2017). In both unmanaged and profit-/yield-maximizing cases, it is not immediately clear whether cycling or chaotic attractors would make fishing patterns more or less resemble BH. Indeed, there is no clear reason to expect that cycling or chaotic attractors would affect the qualitative conclusions of our analysis, but future research could explore this further.

Fourth, we did not consider discounting in our analysis of yield- and profit-maximizing management. If fishery managers discounted profits according to the risk-free market rate of return, for instance, discounting might be an especially important factor affecting management in fast-growing economies such as those in many countries of Costello's (2017) World B. Because discounting decreases the importance of future gains and losses relative to current ones, we hypothesize that discounting should make ecological interactions less influential on the optimal fishing patterns, due to the fact that the indirect effects of fishing via ecological interactions play out over longer time periods than the immediate effects of fishing costs and profits. Thus, discounting may have the effect of moving fishing patterns in the opposite direction—relative to BH—as do ecological interactions. In cases where ecological interactions move yield- or profit-maximizing fishing patterns away from BH, discounting might result in relatively more balanced patterns, especially in World B if its managers used higher discount rates than those in World A. However, these hypotheses remain untested and merit further study.

Together, our results suggest that BH is unlikely to be an optimal management prescription, with respect to yield and profit objectives alone. However, our results do not preclude BH from being a useful high-level strategic heuristic. This could be particularly important for fishery managers and stakeholders concerned by the prospect of western [i.e. Costello's (2017) World A] management strategies being haphazardly applied in other locales [especially Costello's (2017) World B], with potentially deleterious consequences (e.g. see Cao *et al.*, 2017; Szuwalski *et al.*, 2017). BH is also more relevant in situations where even minor changes to the structure of the ecosystem are undesirable, which is analogous to wanting strong conservation constraints in our model. If BH is used as a heuristic for these purposes, though, our results suggest that attention to site-specific nuances (pertaining to the ecosystem, market, etc.) is warranted, as we found such nuances are likely to motivate deviations from BH.

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Appendix A: Analysis of yield or profit maximization in the general case

The first-order conditions for a solution, denoted E^* , to the manager's maximization problems (14) (yield maximization) and (15) (profit maximization) include (A1) and (A2), respectively,

$$q_i B_i(E) + \sum_j q_j E_j \frac{\partial B_j(E)}{\partial E_i} + \sum_j \lambda_j \frac{\partial B_j(E)}{\partial E_i} + u_i = 0, \text{ for all } i, \quad (\text{A1})$$

$$p_i q_i B_i(E) - c_i + \sum_j p_j q_j E_j \frac{\partial B_j(E)}{\partial E_i} + \sum_j \lambda_j \frac{\partial B_j(E)}{\partial E_i} + u_i = 0, \text{ for all } i. \quad (\text{A2})$$

Here, λ_i and u_i are the Lagrange multipliers (often called "shadow values" in economics) corresponding, respectively, to the constraints $B_i \geq L_i$ and $E_i \geq 0$. Each is positive if its corresponding constraint is binding at the optimum and zero otherwise (i.e. $\lambda_i > 0$ if $B_i(E^*) = L_i$; $\lambda_i = 0$ if $B_i(E^*) > L_i$; $u_i > 0$ if $E_i^* = 0$; $u_i = 0$ if $E_i^* > 0$).

If conservation constraints were not binding (i.e. $\lambda = 0$), then each ecological group fished at the optimum (all i for which $E_i^* > 0$, and $u_i = 0$) would be fished at a level (E_i^* for group i) at which the marginal benefits of fishing harder exactly equalled the marginal costs of fishing harder. The marginal benefits of fishing group i harder (denoted MBY_i for a yield objective and MBP_i for a profit objective) are

$$MBY_i = q_i B_i(E^*) + \sum_k q_k E_k \frac{\partial B_k(E^*)}{\partial E_i}, \text{ for all } k \text{ where } \frac{\partial B_k(E^*)}{\partial E_i} > 0, \quad (\text{A3a})$$

$$MBP_i = p_i q_i B_i(E^*) + \sum_k p_k q_k E_k \frac{\partial B_k(E^*)}{\partial E_i}, \text{ for all } k \text{ where } \frac{\partial B_k(E^*)}{\partial E_i} > 0. \quad (A3b)$$

The first of these terms represents the gain in yield or revenue from group i ; the second term represents the gain in yield or revenue from each other group (k) whose abundance increases as group i is fished harder (e.g. prey of group i).

The marginal costs of fishing group i harder (denoted MCY_i for a yield objective and MCP_i for a profit objective) are

$$MCY_i = \sum_l q_l E_l \left| \frac{\partial B_l(E^*)}{\partial E_i} \right|, \text{ for all } l \text{ where } \frac{\partial B_l(E^*)}{\partial E_i} < 0, \quad (A4a)$$

$$MCP_i = \sum_l p_l q_l E_l \left| \frac{\partial B_l(E^*)}{\partial E_i} \right| + c_i, \text{ for all } l \text{ where } \frac{\partial B_l(E^*)}{\partial E_i} < 0. \quad (A4b)$$

The first term represents the lost yield or revenue from all groups (l) whose biomass declines when group i is fished harder [in most cases including group i itself; but see [Abrams \(2009\)](#) for exceptions]. The second term in (A4b) represents the direct costs of increasing fishing effort on group i .

In the case where all prices, costs, and catchabilities are the same across ecological groups (i.e. $p_i = p$, $q_i = q$, $c_i = c$, for all i)—more closely resembling World B—(A3) and (A4), respectively, become (A5) and (A6)

$$MBY_i = q \left[B_i(E^*) + \sum_k E_k \frac{\partial B_k(E^*)}{\partial E_i} \right], \text{ for all } k \text{ where } \frac{\partial B_k(E^*)}{\partial E_i} > 0, \quad (A5a)$$

$$MBP_i = pq \left[B_i(E^*) + \sum_k p_k q_k E_k \frac{\partial B_k(E^*)}{\partial E_i} \right], \text{ for all } k \text{ where } \frac{\partial B_k(E^*)}{\partial E_i} > 0, \quad (A5b)$$

$$MCY_i = q \sum_l E_l \left| \frac{\partial B_l(E^*)}{\partial E_i} \right|, \text{ for all } l \text{ where } \frac{\partial B_l(E^*)}{\partial E_i} < 0, \quad (A6a)$$

$$MCP_i = pq \sum_l E_l \left| \frac{\partial B_l(E^*)}{\partial E_i} \right| + c, \text{ for all } l \text{ where } \frac{\partial B_l(E^*)}{\partial E_i} < 0. \quad (A6b)$$

From (A5) and (A6), we can see that, if all prices, catchabilities, and costs are equal (more closely resembling World B), then how hard group i is fished at the optimum, relative to other groups, would be determined solely by the ecology of the system—i.e.

how fishing on group i impacted the biomasses of all groups (including its own). Ecological groups would be fished harder, in absolute terms, the more resilient (high growth rate) and/or naturally abundant (high carrying capacity) they were, as would groups that suppressed the growth of other groups (e.g. predators, because doing so would increase the biomass of prey), and *vice versa*. However, because ecological groups with high growth rates and carrying capacities would also be more productive, their harvest rate relative to their production (of interest to BH) would often be lower than other groups (see, e.g. [Figure 1a](#)).

If prices, catchabilities, and costs were unequal (World A), optimal fishing patterns—with either a yield or a profit objective—would promote relatively higher yields (i.e. higher biomass \times fishing effort) in “higher-value” ecological groups (defined as those with higher prices and catchabilities and lower costs). The exception is that catchability (q_i) differences do not affect the optimal fishing mortality for yield maximization (though they do still affect the optimal effort), because there is no yield cost to greater effort (but there is a profit cost). For either yield maximization or profit maximization, we would generally expect fishing on a group to be disproportionately increased, in World A relative to World B, if the group ecologically suppressed the biomass of higher-value groups, and *vice versa* if it ecologically enhanced the biomass of higher-value groups. However, we might expect this effect to be larger for yield objectives, since the economic cost of culling such groups would not be factored in (e.g. [Figure 1c](#)).

As discussed in the main text, ecological factors and economic factors should tend to deviate the optimal pattern away from BH in the same directions—relative to production, more towards large-bodied predators, with lower carrying capacities and higher prices—with some subtleties such as illustrated in [Figure 1f](#). Thus, we would expect World A’s optimal fishing pattern to typically deviate more from BH than World B’s. Moreover, from (A3) and (A4), we can see that the first-order conditions would only be satisfied at the same biomass for all groups (BH in our model) under extremely restrictive conditions—either all groups are ecologically and economically identical or they differ in ways that exactly cancel out (see [Figure 1](#)).

If the conservation constraint binds for ecological group i , then this implies that $B_i < L_i$ at the unconstrained optimum. Since $B_i = S_i/F_i$ at equilibrium [by (1)], imposing a conservation constraint on group i thus either reduces (if the constraint binds), or does not change (otherwise) F_i/S_i . For conservation constraints to deviate the optimal fishing pattern further from BH than the unconstrained optimum would require the constraints to bind on groups with F_i/S_i already lower than groups for which the constraints would not bind. While not impossible (the conservation constraints are subjectively determined in our model), this scenario seems unlikely. Far more likely is the scenario where conservation constraints bind on the most depleted ecological groups (with highest F_i/S_i), and thus the constraints move the optimal fishing pattern towards BH.