Effect of fishing intensity and selectivity on trophic structure and fishery production

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ABSTRACT: Fishing intensity and selectivity patterns affect ecosystem structure and fisheries yield, the 2 fundamental performance measures in the ecosystem approach to fisheries. We used a simple multispecies predation model to explore the effect of alternative fishing strategies on a 3-trophic-level food chain. Fishing strategies included highly selective fishing, nonselective fishing, and balanced harvesting that harvests all species at an instantaneous fishing mortality rate either proportional to intrinsic population growth rate or proportional to current population growth rate. The results showed that harvesting species at higher trophic levels has a low impact on total biomass but results in very low yields and severe impacts on trophic structure. Selectively harvesting species at the bottom of the food chain reduces the biomass of all fish, results in high yields, and is the only strategy that maintains unfished trophic structure. Non-selective fishing produces high total yield, but can cause extinction of fish at high trophic levels, and severely alters the trophic structure. Balanced harvest strategies produce higher total yield than harvesting species only at the bottom of the food chain, and have a smaller impact on trophic structure than selectively harvesting the top predator or nonselective fishing, but cannot fully maintain trophic structure. While these findings from a very simple model can provide insight into results from more complex models, analysis of sensitivity to structural assumptions in such simple models will be required to shed further light on the dynamic consequences of fishing across multiple trophic levels.

KEY WORDS: Holling-Tanner model · Lotka-Volterra model · Ecosystem approach to fisheries · Trophic structure · Multispecies harvest strategies · Balanced harvest

INTRODUCTION

Fisheries traditionally target a small number of economically valuable species, mostly at higher trophic levels. Such a highly selective fishing pattern across the ecosystem has been intensified by various regulations and policies that encourage reducing bycatch of low-valued species and prohibiting catching small fish. These fishing practices, together with high fishing intensity, have had grave unintended impacts on marine ecosystem structure and biodiversity. Intensive fishing of economic species has caused overfishing of many commercial species (Worm et al. 2009, Costello et al. 2012). In the past 2 decades, eco-

system-based management has been proposed to deal with these issues (Garcia et al. 2003). A key feature of the ecosystem approach to fisheries (EAF) is to conserve ecosystem structure and biodiversity while extracting food and gaining other economic services (FAO 2003). Maintenance of ecosystem structure has become one of the most important goals in fisheries management. High-level management policy-makers, from the United Nations to individual states, have unanimously adopted this goal through the Convention on Biodiversity (SoCBD 2004).

To reduce the ecological effects of fishing while increasing food production, the concept of balanced harvest (BH) was recently proposed (Zhou et al. 2010,

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Garcia et al. 2012). The idea is to apply fishing mortality proportional to the natural productivity of each component in the marine ecosystem and to increase food security by utilizing as many species as possible. Simulation studies have shown that BH can better preserve ecological structure, increase ecosystem stability, and at the same time increase fisheries production (Garcia et al. 2012, Law et al. 2012, 2015, Rochet & Benoît 2012, Jacobsen et al. 2014, Kolding et al. 2016b). These studies used size-based models or whole ecosystem models. Recently, there has been increased debate about, and considerable criticism of the BH concept (Burgess et al. 2016, Froese et al. 2016, Garcia et al. 2016, Pauly et al. 2016). For example, the size-spectrum models used to examine BH have been criticized as being unrealistic (Andersen et al. 2016, Froese et al. 2016), and it has been strongly recommended that various types of modeling tools are required to investigate the pros and cons of BH (Garcia et al. 2014). As trophic structure is fundamental to the understanding of ecosystem structure, it is also necessary to understand how alternative fishing patterns and intensity affect trophic structure and fisheries yield. Such a study requires a multispecies model.

Among a range of multispecies models, the Lotka-Volterra predation equations have been studied extensively (Brown & Rothery 1993). The classic Lotka-Volterra equations involve 2 species with predation being a linear function of prey density (Holling type I functional response). The models also assume a completely coupled system by making the amount of prey consumed directly proportional to the amount of biomass increase of the predator, with or without taking ecological transfer efficiency into account. This classic model has been extended to study more complicated systems. One extension of the basic model investigates alternative functional responses for describing the relationship between the feeding rate of a predator and its food density. For fish species, studies found that the Holling type II functional response more accurately predicted the observed functional response and was superior to the type I model (Murray et al. 2013). Type II functional response is typically used for fish predation (Kar & Ghosh 2013, Ghosh & Kar 2013a, Ghosh et al. 2014, Walters et al. 2016). Another extension expands the 2-species models to multispecies models. Within this form of extension, a 3-species food chain model has become an active theoretical research area (Hastings & Powell 1991, Chauvet et al. 2002, Naji & Balasim 2007, Wang et al. 2007, Lv & Zhao 2008, Mamat et al. 2011). These studies attempt to model 3 trophic levels using the classic Lotka-Volterra equations with a fully coupled system. These types of models exhibit many forms of complex behaviors (including multiple stable states, chaotic dynamics, and strange attractors). Stable equilibria may be possible but only when all parameters are fixed together and meet stringent conditions (Chauvet et al. 2002, Lv & Zhao 2008, Sunaryo et al. 2013).

Alternative multispecies models have been developed and used in fisheries research (see reviews by Whipple et al. 2000, Plagányi 2007, Rose & Sable 2009). Among these, a modified Lotka-Volterra model in the form of Schaefer's logistic equations, which avoids the limitation of the classical Lotka-Volterra model to describe many realistic phenomena in biology (Peng & Wang 2005), has been widely used to investigate predation among species (May et al. 1979, Beddington & Cooke 1982, Spencer & Collie 1996, Gamble & Link 2009, 2012, Ghosh & Kar 2013a). These models vary in several ways; some assume a linear predation functional response, which is often called the Leslie-Gower model (Hsu & Huang 1995, Gamble & Link 2009), while others assume nonlinear functions such as a Holling type II functional response, which is often called the May model or Holling-Tanner model (Tanner 1975, Brown & Rothery 1993, Peng & Wang 2005, Ghosh & Kar 2013a); some use a fixed carrying capacity for each species (Ghosh & Kar 2013b), while others link the carrying capacity of a predator to the abundance of its prey (May et al. 1979, Hsu & Huang 1995, Ghosh & Kar 2013a). One of the main advantages of these models is that they adopt a nonlinear population growth formulation similar to the Graham-Schaefer surplus production model that is familiar to fisheries biologists and can be easily linked to the idea of balanced exploitation by applying a fishing mortality rate proportional to productivity, production, or biomass.

The objective of this paper was to use the simple Holling-Tanner model to investigate how fishing intensity and selectivity affect biomass, yield, and trophic structure. Like several other studies using predation models (May et al. 1979, Beddington & Cooke 1982, Brown & Rothery 1993, Ghosh & Kar 2014), we considered simple models for harvesting interacting populations in a theoretical community, and focused on the general qualitative effects of alternative fishing strategies, rather than on specific quantitative predictions. Because we were particularly interested in insights into the concept of balanced harvest, the models are cast as highly simplified metaphors for a 3-trophic-level system.

MATERIALS AND METHODS

We assumed a 3-trophic-level fish community, where level 1 represents planktivorous fish. Because we were only interested in fish, and ignored true primary producers such as phytoplankton, we refer to this trophic level as trophic level 1 (TL1). Trophic level 2 (TL2) consists of small intermediate trophic level piscivorous fish, and trophic level 3 (TL3) consists of large apex predators. Such a community is simple enough to track population dynamics and ensure model convergence, but complex enough to investigate trophic effects of fishing. Further, we assumed that food is limiting at TL1 by assigning a fixed carrying capacity, but that carrying capacity varies at TL2 and TL3 according to their varying prey abundance.

We did not divide life history into multiple stages, even though species at lower trophic levels may prey on small juveniles whose adults are at higher trophic levels within a narrow window of their life history (e.g. feeding on eggs and larvae of species at high trophic levels). By considering a species as an ecological unit, the overall net energy always transfers from TL1 to TL2 and from TL2 to TL3. In such a gross characterization of whole food webs, it can be argued that body size is embedded in the process as body size tends to increase with trophic level (Jennings et al. 2001, McCann et al. 2016).

The classic Holling-Tanner model is described as follows. For trophic level i, the rate of change in population (biomass), dB_i/dt, can be expressed as:

$$\frac{dB_i}{dt} = G_i - P_{i,i+1} - C_i \qquad (1)$$

where G is population growth, P is loss due to predation, and C is loss due to catch (harvest). The subscripts represent trophic levels or their interaction, e.g. $P_{1,1+1}$ refers to predation of TL1 prey by TL2 predator. For TL1:

$$G_1 = r_1 B_1 \left(1 - \frac{B_1}{K_1}\right) \qquad (2)$$

The population growth term G is a general logistic equation as commonly used in biomass dynamics models, where r is the intrinsic population growth rate (productivity parameter), and K is the carrying capacity. Parameter r is known to be regulated by life history traits. To investigate prey–predator interactions, the amount of predation P is treated separately from population growth (McCann et al. 2016, Walters et al. 2016). As there is only one prey species, so no prey switching, P is modeled as a Holling type II functional response:

$$P_{1,2} = \frac{p_{1,2} B_1}{D_1 + B_1} B_2 \qquad (3)$$

where $p_{1,2}$ is the maximum rate of predation, and p/D measures the predation rate at low prey density where D is the biomass when the predation rate reaches half of its maximum (Brown & Rothery 1993). Fishing mortality is $C_1 = F_1 B_1$.

In the Holling-Tanner model (Brown & Rothery 1993, Braza et al. 2003, Wang et al. 2008, Maiti & Pathak 2009, Cao et al. 2013, González-Olivares et al. 2016), the rate of population change at TL2 is:

$$\frac{dB_2}{dt} = r_2 B_2 \left(1 - \frac{B_2}{e_{1,2} B_1}\right) - \frac{p_{2,3}}{D_2 + B_2} B_2 B_3 - C_2 \qquad (4)$$

The first component on the right side of Eq. (4) is population growth similar to Eq. (2). The population dynamics at TL2 are affected by food limitation at the lower trophic level (TL1) and predation from the higher trophic level (TL3). Population growth G is regulated by available prey biomass B_1 and energy transfer efficiency parameters $e_{1,2}$. These 2 variables replace carrying capacity K_2 in the production model as TL2 reaches its maximum biomass by converting all prey biomass B_1 into its own biomass. It is equivalent to $(P/B)B$ in Ecopath (here P is production) where the P/B ratio is typically a fixed input for each functional group (Heymans et al. 2016). The second component in Eq. (4) is predation similar to Eq. (3), and the last term is fishing mortality.

The rate of population change for species at TL3 is:

$$\frac{dB_3}{dt} = r_3 B_3 \left(1 - \frac{B_3}{e_{2,3} B_2}\right) - M_3 B_3 - C_3 \qquad (5)$$

To be consistent with species at lower trophic levels, a small predation mortality M_3 is included in the equation, as apex species (such as sharks) are still subject to some level of 'natural' mortality, e.g. predation by species not in the model. The Holling-Tanner model extends the Lotka-Volterra model by incorporating more realistic components for the interaction of predator and prey (Brown & Rothery 1993, Hsu & Huang 1995). In addition to the Holling type II equation as a functional response relating predation rate to prey density, the growth component is a nonlinear function of prey biomass. This nonlinearity is interpreted as a complex situation involving many factors such as the effect of food intake on survival and reproduction, and competition amongst the predators for food and other resources (Brown & Rothery 1993).

We carried out informal sensitivity tests for several key input parameters independently but did not include the results in the paper because our objec-

tive was to explore general qualitative patterns of response rather than parameter sensitivity. Arbitrary parameter values are typically used in similar studies, such as any value between 0 and 1 (Brown & Rothery 1993, Matsuda & Abrams 2006, Kar & Ghosh 2013, Ghosh & Kar 2014). Here, we chose reasonable parameters to ensure species co-existence when there is no fishing, as well as biologically realistic values (Table 1). In general, the models are less sensitive to K, r, D, and M, as the patterns or trends (but not the exact numbers) in biomass, yield, and structure remain similar. We tested a wide range of values, e.g. r from 0.1 to 10, D from 0 to 500 000, and observed similar qualitative outcomes. Among 454 fish species caught in Australia's Southern and Eastern Scalefish and Shark Fishery, r can be estimated for 208 species from FishBase or other literature (Zhou et al. 2011). Their r values range from 0.057 to 2.84 with a mean 0.94 and a SD 0.55. Note that in the Holling-Tanner model, predation mortality P is not included in the production term as it is in the Schaefer production model. Such a separation is necessary for studying prey–predator interaction. As such, r here must be greater than in the Schaefer model. Assuming predation contributes to 50% of r, the mean r before predation would be about 1.88. Since r typically decreases as trophic level increases, we chose 2, 1, and 0.25 (yr^{-1}) for the 3 trophic levels. We chose a value of D not too large or too small from the initial biomass. Altering the p value across a wide range from 0.001 to 100 may cause the shape of indicator curves (biomass and yield) to change, but the qualitative patterns across trophic levels remain similar. As this parameter is rarely measured, we again chose a value that simply ensures co-existence of all species when there is no fishing. The most sensitive parameter appears to be ecological efficiency, e, that may prevent constructing a functional community (e.g. energy transfer efficiency $e > 0.3$ results in zero biomass for one or more species even without fishing). From 48 trophic models of aquatic ecosystems, the estimated energy transfer efficiency ranges between 0.02 and 0.24 (Pauly & Christensen 1995). We tested the sensitivity of our model to changes in e within this range and found little effect on the qualitative conclusions. We did not include either parameter uncertainty or random variability within the simulations as the focus was on qualitative results.

The differential equations (1), (4), & (5) were simultaneously solved for population sizes at each trophic level. We explored the following 6 cases (fishing strategies) by varying fishing intensity and selectivity across species (and hence trophic levels). Except Cases 4 and 6, fish are harvested at an instantaneous fishing mortality rate F proportional to their intrinsic growth rate r, i.e. $F_i = fr_i$ and $C_i = fr_iB_i$. The constant f is a scalar varying between 0 and 1.

(1) Selectively harvest TL3 only: $F_3 = fr_3$ and $F = 0$ for TL1 and TL2.

(2) Selectively harvest TL2 only: $F_2 = fr_2$ and $F = 0$ for TL1 and TL3.

(3) Selectively harvest TL1 only: $F_1 = fr_1$ and $F = 0$ for TL2 and TL3.

(4) Non-selective harvest: harvest all TLs in proportion to their biomass so each fish has the same probability of being caught, regardless of trophic level i.e. $F_i = f$ and $C_i = F_iB_i = fB_i$.

(5) Balanced harvest 1 (BH1): harvest all TLs with F proportional to intrinsic productivity, i.e. $F_i = fr_i$ and $C_i = fr_iB_i$.

(6) Balanced harvest 2 (BH2): harvest all TLs with catch proportional to their production (= growth of population biomass), i.e. $C_i = F_iB_i = fG_i$. Because G_i is smaller than the standing biomass B_i, at the same f fishing mortality rate F_i (= fG_i/B_i) is smaller than F_i in other cases.

In all the scenarios, the fishing intensity scalar f systematically increases from 0 to 1 in 100 equal

Table 1. Parameters and their assumed values used in the simulations. TL: trophic level

Parameter (units)	Notation	Value
K_1 (weight)	Initial carrying capacity for TL1	1000
r_1, r_2, r_3 (yr^{-1})	Intrinsic growth rate at low density for species at TL1, TL2, and TL3	2.0, 1.0, 0.25
$p_{1,2}$, $p_{2,3}$ (yr^{-1})	Maximum predation rate. The first subscript is the prey and the second is the predator	0.5, 0.5
D_1, D_2 (weight)	Parameter affecting the slope of Holling Type II functional response	100, 10
$e_{1,2}$, $e_{2,3}$ (dimensionless)	Ecological energy transfer efficiency	0.2, 0.2
M_3 (yr^{-1})	Natural mortality for species at TL3	0.01
F_1, F_2, F_3 (yr^{-1})	Instantaneous fishing mortality rate	From 0 to r
f (dimensionless)	Ratio between F and r	From 0 to 1

steps. The key performance measures for this study include (1) biomass (population size), (2) equilibrium yield, and (3) trophic structure. To compare the results across 3 trophic levels, we used relative quantities by scaling the biomass and yield to the maximum value for that trophic level so that relative biomass and yield fall between 0 and 1. Trophic structure is quantified by 2 measures, the slope of biomass over trophic levels, and a disturbance index, DI. The first measure (slope b) is obtained from $\log(B_i) = a + bTL_i$ (Kolding et al. 2016a). To compare across all f levels in the figures, the b value at $f = 0$ (slope when there is no fishing) is subtracted from the raw b. The second metric DI is the sum of the absolute difference between the biomass ratio of adjacent trophic levels, and its reference ratio when there is no fishing:

$$DI = \sum_{TL} \left| \frac{B_{TL+1,f}}{B_{TL,f}} - \frac{B_{TL+1,0}}{B_{TL,0}} \right| \tag{6}$$

This formulation is similar to the disturbance index used by Bundy et al. (2005), but here the biomass ratio is between 2 adjacent trophic levels rather than a fraction of the total biomass. Changes in the numerical relationship between trophic levels are direct measures of disturbance to trophic (ecosystem) structure and population evenness. Ideally, fishing should not alter b and DI, and the smaller the change in these indicators, the less impact of fishing on trophic structure.

RESULTS

Case 1: selectively harvest TL3 only

When predation interactions are included, harvesting the species at TL3 reduces its biomass and releases TL2 from predation (Fig. 1a). Increased TL2 biomass in turn causes its prey biomass to decline (due to its large biomass, the change in TL1 is relatively small). Hence, harvesting TL3 causes a cascading effect at lower trophic levels. Under a constant fishing intensity (i.e. a fixed F every year), the community eventually reaches a new equilibrium, which may take a few time steps (years) or several hundred years depending on fishing intensity and selectivity patterns. The cascading impact dampens from one trophic level to the next. The yield exhibits a dome-shaped curve (Fig. 1b), with the maximum sustainable yield occurring at $F = 0.5r$ ($f = 0.5$).

Selectively harvesting TL3 also affects trophic structure (Fig. 1c). The impact on structure intensifies as f increases: slope b deepens while DI increases.

Case 2: selectively harvest TL2 only

Selectively harvesting TL2 reduces its biomass, which in turn releases TL1 from predation but reduces available food for TL3 (Fig. 2). As a consequence, equilibrium biomass at both TL2 and TL3 declines while it increases at TL1. At extremely high
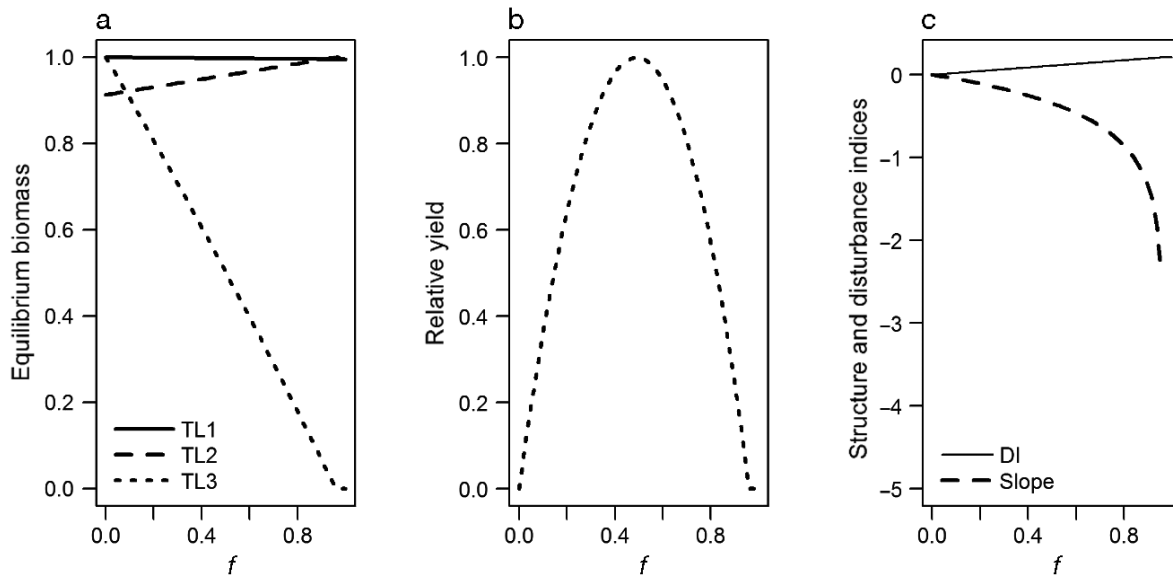

Fig. 1. Equilibrium biomass, yield, and trophic structure for Case 1, harvesting apex predator at trophic level (TL) 3 only. (a) Relative equilibrium biomass (maximum = 1.0); (b) relative yield (maximum = 1.0); (c) slope of biomass over trophic level (TL), and disturbance index (DI)
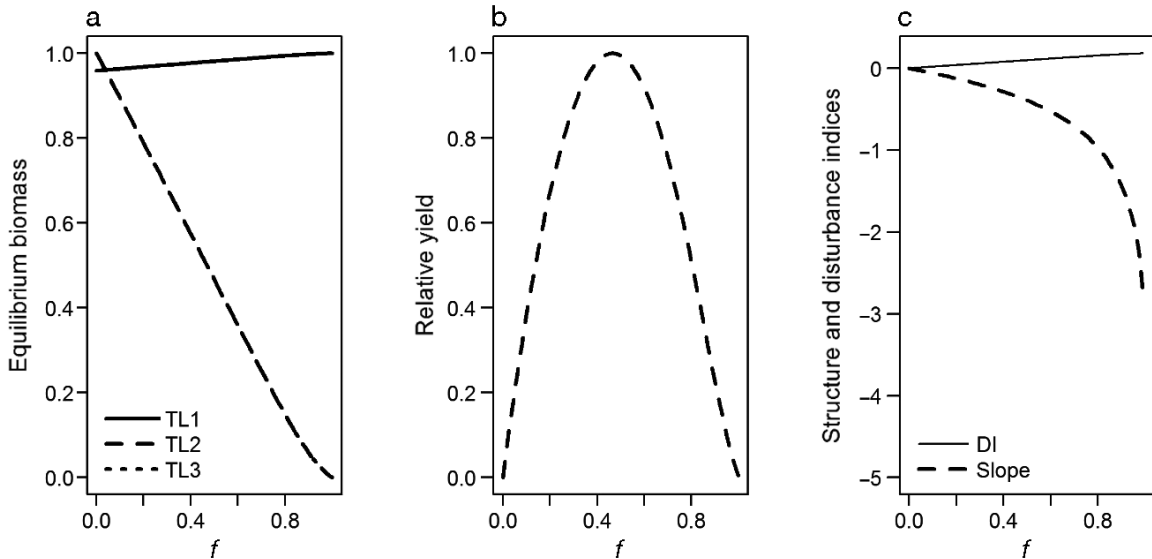
Fig. 2. Case 2: harvesting trophic level (TL) 2 only. The lines of equilibrium biomass for TL2 and TL3 are superimposed. Legends as in Fig. 1

fishing intensities, B_2 and B_3 drop to zero, and TL1 reaches its carrying capacity. The decline in B_2 results in an exactly proportional decline in B_3 as fishing intensity increases. Similar to Case 2, slope b declines and DI increases.

Case 3: selectively harvest TL1 only

Harvesting fish at the bottom of the food chain (TL1) has an impact not only on themselves but also all trophic levels above. Even though fish at higher trophic levels are not harvested, their biomass naturally declines due to food limitation (Fig. 3). This is a

cascade effect passing from TL1 to TL2 to TL3. The maximum yield occurs close to $F_1 = 0.5r_1$. There is little change in slope b and DI over a wide range of f, except at very high fishing intensity (well beyond that required to maximize yield for TL1) where these parameters are sensitive to low biomass (Fig. 3c).

Case 4: non-selective fishing

Since population growth rates vary among trophic levels, the one that has the lowest growth rate (TL3) becomes extinct first as f increases (Fig. 4). Biomass at TL1 declines to a half of the carrying capacity ($K/2$)
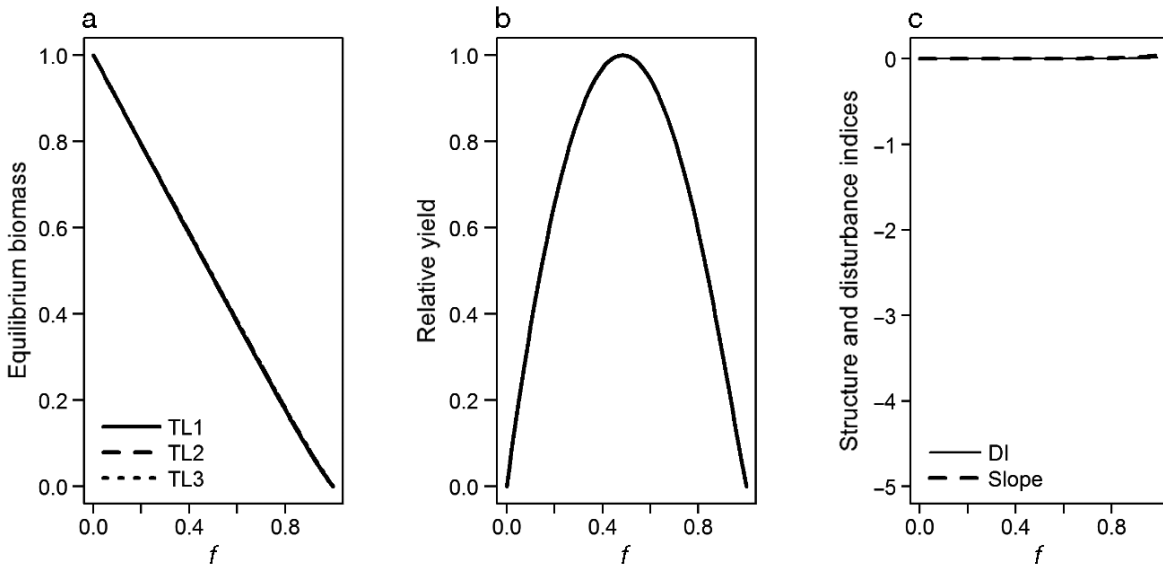

Fig. 3. Case 3: harvesting trophic level (TL) 1 only. The lines of equilibrium biomass for all trophic levels are superimposed. Legends as in Fig. 1
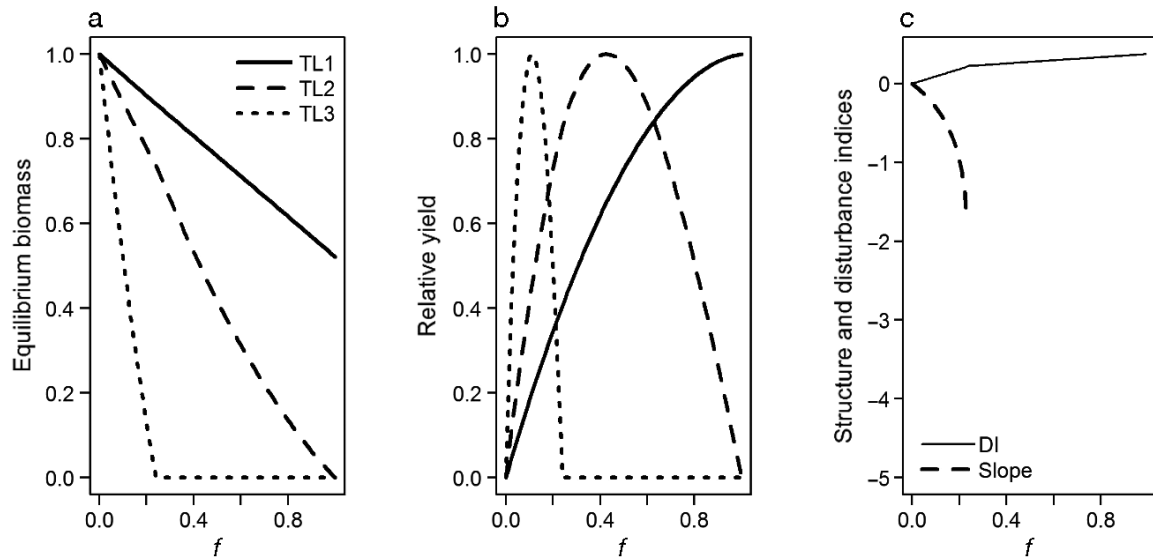
Fig. 4. Case 4: non-selective fishing by harvesting all trophic levels (TLs) in proportion to biomass. Legends as in Fig. 1

when $f = 1$. This can be easily shown from the rate of change $dB_1/dt = r_1B_1(1 - B_1/K) - fB_1$ because $r_1 = 2$ and predation from TL2 and TL3 becomes nil. As a result, yield from TL1 continues to increase as f increases (Fig. 4, middle panel). The species at the top of the food chain become extinct at a relatively low fishing intensity ($f < 0.3$). Clearly, the trophic structure is greatly affected.

Case 5: Balanced harvest (BH1)

As f increases, equilibrium biomass at all trophic levels declines, but the decline is faster at higher than at lower trophic levels (Fig. 5). This is because when fishing reduces biomass at a lower trophic level, the available food for fish at higher trophic levels diminishes, leading to a proportional decrease in biomass. On top of this natural consequence, any level of additional mortality from fishing, even though in proportion to their productivity, triggers further population declines at higher trophic levels. When fishing intensity increases, biomass at higher trophic levels is depleted more quickly than at lower trophic levels. Except for TL1, maximum yield occurs at low fishing intensities ($f < 0.5$), and the higher the trophic level, the lower the relative F/r ratio (Fig. 5b). This is due to the non-linear concave equilibrium relationship be-
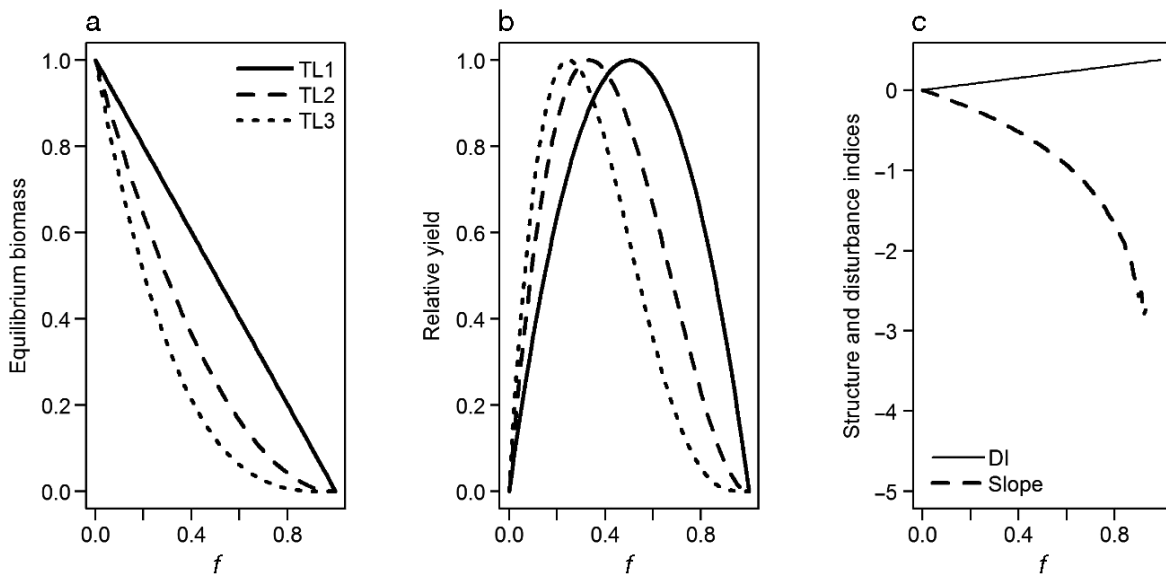

Fig. 5. Case 5: balanced harvest 1 (BH1) by harvesting all fish at instantaneous fishing mortality rate F proportional to intrinsic productivity. Legends as in Fig. 1

tween biomass and fishing intensity (Fig. 5a). Consequently, slope b decreases and DI increases. However, in contrast to Cases 1, 2, and 4, BH1 does not drive fish at particular trophic levels extinct first. Extinction occurs simultaneously to all fish when $f = 1$. Interestingly, trophic structure cannot be maintained and both b and DI deviate from 0 as f increases.

Case 6: Balanced harvest (BH2)

In contrast to BH1, fishing mortality rate here is proportional to current productivity for each trophic level while the catch is proportional to the current production, G. Under this strategy, equilibrium biomass at a higher trophic level also declines more quickly than at a lower trophic level (Fig. 6).

Because growth is density-dependent, yield continues to increase as population declines until catch becomes a very large proportion of the production ($f > 0.8$) (Fig. 6b). As f increases further, yield drops quickly because the population crashes. Proportionally removing production causes very small changes in trophic structure (b and DI) over a wider range of f (Fig. 6c). Similar to BH1 and in contrast to Cases 1, 2, and 4, BH2 does not drive fish at a particular trophic level to extinction first. Extinction occurs simultaneously to all fish at extremely high fishing intensity.

Overall biomass and yield

We examined each individual strategy above. It is also valuable to compare total biomass and total yield from all trophic levels under alternative fishing patterns and their impact on structure. The comparison is based on increasing fishing mortality rate F rather than scalar f (Fig. 7). Note that F varies from 0 to r (extinction) so the values are TL-dependent, i.e. 0 to 2 for TL1, 0 to 1 for TL2, and 0 to 0.25 for TL3. For non-selective fishing, BH1, and BH2 (Cases 4 to 6), fishing mortality F is calculated as total yield divided by total biomass across all trophic levels.

From Fig. 7, as well as Figs. 1 to 6, we conclude:

(1) Harvesting species at higher trophic levels (TL3 and TL2) has a low impact on total biomass because of the bottom-heavy biomass pyramids, and because the catch is very small. In addition, harvesting predators increases prey biomass by releasing predation pressure. Because of relatively low biomass and low growth rate at higher trophic levels, the yield from them is very low, particularly at TL3.

(2) Selectively harvesting TL1 reduces biomass of all fish through food limitation available to higher trophic levels. Because of high productivity and biomass, yield from TL1 can be high (but not necessarily the economic profit, see 'Discussion'). More importantly, this is the only fishing strategy that can maintain trophic structure measured by slope and DI across a wide range of fishing pressures (Fig. 7).

(3) Non-selective fishing results in high total yield. However, this fishing pattern causes extinction to fish at TL3 and TL2 long before TL1 is depleted, severely altering trophic structure.

(4) Balanced harvest, either BH1 or BH2, has a similar effect on total biomass as non-selective harvesting and produces higher total yield than harvesting TL1. Although BH has a smaller impact on structure
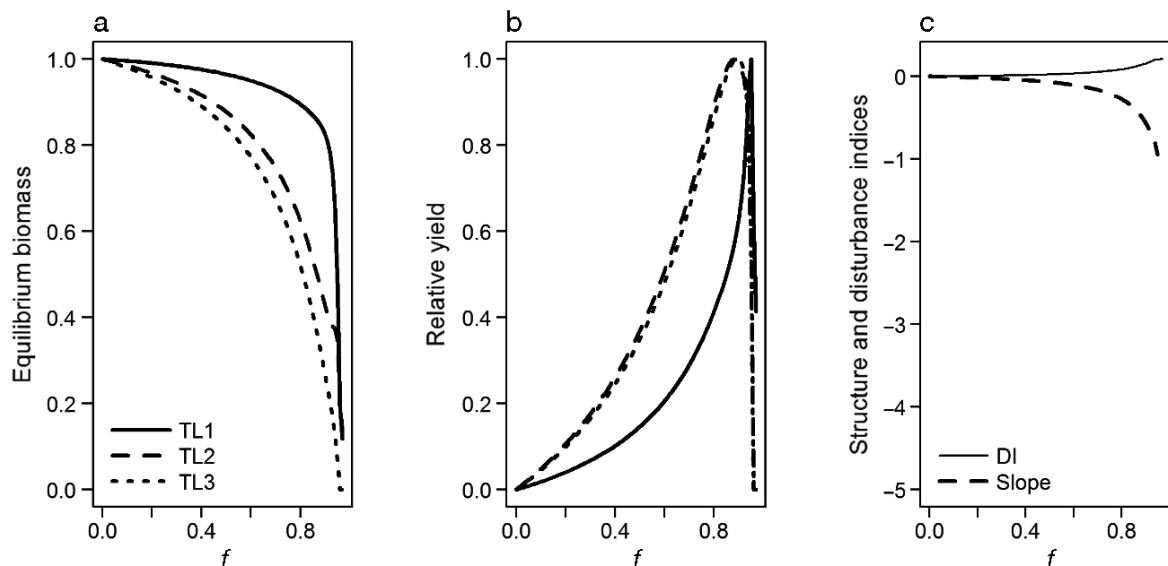

Fig. 6. Case 6: alternative balance harvest (BH2) by harvesting all fish proportional to production. Legends as in Fig. 1
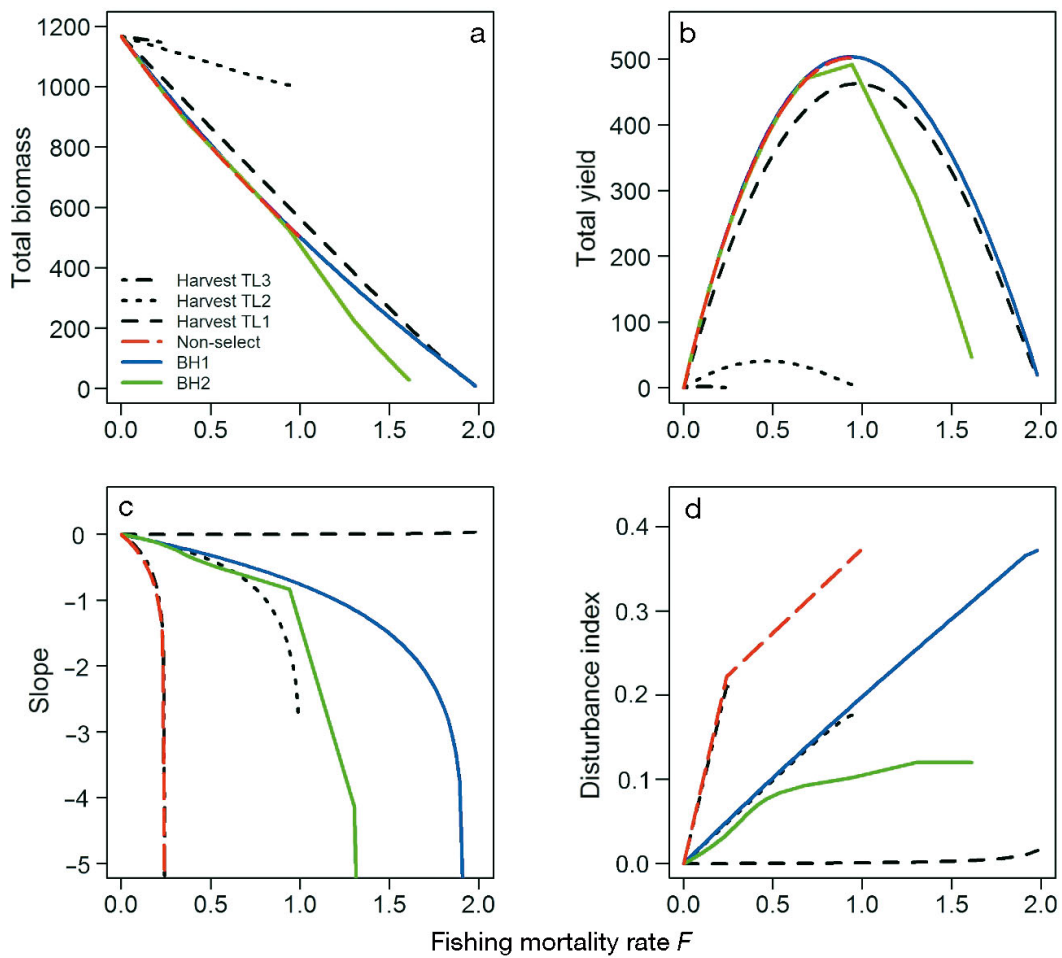
Fig. 7. Comparison of total biomass, total yield, and trophic structure measured by slope and disturbance index over fishing mortality rate across all trophic levels (TL) at equilibrium for alternative fishing scenarios. Harvest TL1 to TL3 selectively harvests only one trophic level

than selectively harvesting top predators or non-selective fishing, unfortunately, it cannot fully maintain trophic structure.

DISCUSSION

We used a simple Holling-Tanner type predation model to explore 6 fishing scenarios to investigate how fishing pattern and intensity may affect biomass, yield, and trophic structure in a fished ecosystem. This classic model formulation has been widely used for studying fish species interactions (May et al. 1979, Beddington & Cooke 1982, Gamble & Link 2009, 2012, Takashina et al. 2012, Ghosh & Kar 2013a,b). This is the first of 4 modeling approaches (the other 3 being multispecies virtual population analysis, Ecopath with Ecosim, and multispecies bioenergetic models) recommended for multispecies modeling

(Latour et al. 2003). We do not argue that this type of model is more realistic than other formulations, since it is well known that no mathematical model can truly describe the complex dynamics of an eco-system. As such, a large range of models is needed to obtain a deeper understanding of complex ecosystem processes and to determine whether different models could reach similar qualitative conclusions (Garcia et al. 2014). While the new concept of BH has been examined by size-based models (Law et al. 2012, 2016, Rochet & Benoît 2012, Cohen et al. 2012, Jacobsen et al. 2014) and complex ecosystem models (Garcia et al. 2012, Kolding et al. 2016b), no simple multi-species model has been used to investigate BH to date. We recognize that there are various multi-species models that are extended from classic Lotka-Volterra models, but we only focused on the most common one in this study as a starting point for evaluating BH and other fishing strategies. The model

itself is not new, but the wide range of cases (types of fishing patterns across the ecosystem) examined in this study is uncommon in the existing literature. Simple predation–prey models continue to be used in fisheries research (McCann et al. 2016, Moffitt et al. 2016, Walters et al. 2016). Of course, complex ecosystem models such as Ecopath with Ecosim are also useful for such a theoretical study, as used in Garcia et al. (2012). However, 'it would be a grave mistake to assume that the more optimistic predictions from more complex ecosystem models are better simply because they represent ecosystem structure and large-scale spatial organization in more detail than the simpler models' (Walters et al. 2016, p. 273).

It is obvious that fishing should affect biomass and fisheries yield, but the effect of fishing pattern on trophic structure is less clear. For most selectivity patterns examined in this study, as fishing intensity increases, biomass at higher trophic levels declines faster than biomass at lower trophic levels, so the slope of the biomass spectrum deepens. A notable exception is Case 3, where only the lowest trophic level is harvested. In this case there is little change in trophic structure, because all fish are negatively affected by biomass reduction at the bottom of the pyramid. For this model at least, fish at higher trophic levels suffer from diminished food supply at the same rate of fishery removal, preserving the overall trophic structure. This situation may become more complicated when there are multiple species at the same trophic levels, and predators are generalists that consume prey over multiple trophic levels.

If the management aim is for high fishery production and low impact on ecosystem structure, the best strategy is to selectively harvest fish at the lowest trophic level possible. The lower the trophic level, the higher the productivity and production, the higher the yield, and the less energy loss through the ecological process. With this fishing pattern it is possible to 'maintain ecosystem structure' while extracting a relatively large amount of food from the system. The results seem to contradict the idea of harvesting a slice of the ecological pyramid to preserve the shape of the pyramid (Jul-Larsen et al. 2003, Bundy et al. 2005). However, when we consider prey–predator interactions, the results of Case 3 make sense for the model used. Constantly removing a fixed fraction of biomass at the lowest consumable trophic level reduces the same fraction of the population at all higher trophic levels simply due to food limitation, resulting in no overall change to the pyramid shape. This follows from the assumption in the model that carrying capacity at higher trophic levels is propor-

tional to (current) biomass at the next lowest level. As a consequence, species at higher trophic levels adjust their abundance accordingly in proportion to the reduction at the lower trophic levels. This scenario produces high yield, only slightly lower than the non-selective fishing and the 2 BH scenarios.

However, in this study we did not take economics into consideration. In current markets, larger predatory fish often sell at higher prices. If this economic factor is accounted for, there appears to be no single fishing strategy that can simultaneously achieve large biomass, high yield, low ecological impact, and high economic profit. Selectively harvesting fish at the bottom of the trophic chain may accomplish the first 3 objectives, but these are typically small fish with relatively low economic value. Harvesting fish solely at low trophic levels is unlikely to be commercially acceptable to the fishing industry, at least given current consumer preferences.

On the other hand, the above economic discussion is from a micro-economic point of view that addresses profitability of fishing companies. From an ecosystem perspective, BH concerns the structure and function of the whole ecosystem rather than a subset of target species. From a food security and social-economic benefit perspective, BH concerns the long-term benefit to society as a whole, rather than just short-term profit to a subset of society such as fishing companies. Species with a lower abundance may attract a higher market price, but do not necessarily possess higher nutritional value, which may be the ultimate benefit to the society.

Ignoring economic considerations, fishery management that strives to selectively harvest a few target species at higher trophic levels (Cases 1 and 2) is flawed both in protecting ecosystem structure and in achieving high total food production. In typical marine food webs, the higher the trophic level, the lower the abundance and growth rate (Trebilco et al. 2013). Any additional mortality from fishing will necessarily reduce populations further at higher trophic levels and increase populations at lower trophic levels due to diminished predation. Extensive evidence supports the conclusion that biomass of large fish and top predators has declined from unfished levels much more than small fish and species at lower trophic levels (Restrepo 1992, Friedlander & DeMartini 2002, Benoît & Swain 2008, Lotze & Worm 2009, Tremblay-Boyer et al. 2011, Christensen et al. 2014).

A non-selective fishing pattern (Case 4) can also achieve high total yield, but causes severe structural change and drives low productivity species extinct at relatively low fishing intensity. As such, the high total

biomass and total yield are composed mainly of small fish from low trophic levels as a consequence of eliminating predators at high trophic levels (McCann et al. 2016, Szuwalski et al. 2017).

To alleviate fishing impacts on biodiversity and ecosystem structure while enhancing total yield, BH suggests reducing fishing pressure on highly targeted species and redistributing a moderate fishing pressure to a wider range of ecosystem components. As illustrated above and discussed elsewhere in the literature, there are potentially alternative approaches within this framework, but exactly how to allocate fishing pressure over trophic level, species, and size is not straightforward and requires further research. For example, balancing over body size based on size-spectrum models and suggesting harvesting small juvenile fish have received strong critiques (Froese et al. 2016).

Clearly, research and debates on the concept of BH continue. The key concept underlying BH is to apply fishing mortality in proportion to the natural productivity of each ecological component. The sensitive issue is what ecological components should be considered. We categorize several levels of BH: (1) balancing (i.e. applying fishing pressure proportional to natural productivity) within a group of species (e.g. commercial species); (2) balancing all species within a community, including non-target species; (3) balancing across body sizes regardless of species; and (4) balancing across species and sizes. Level (1) is what conventional maximum sustainable yield (MSY)-based fishery management aims to achieve. Hence, at this level BH is not a new idea but has been adopted by modern fisheries for over half a century. Although BH stresses the importance of ecological interactions between species, this is also not new as conventional management has increasingly attempted to take ecological interaction into account. The possible difference is that BH does not specifically define MSY as a target, but rather as a potential limit. From an ecosystem point of view, applying proportional fishing pressure to species beyond current commercial species (level 2) is simply a natural extension of an MSY-based strategy. On the other hand, balancing across sizes at levels 3 and 4 (for example, suggesting juvenile harvest) is less straightforward. Research on this type of BH yields inconsistent conclusions (Andersen et al. 2016) and requires more research, but is not a focus of this paper.

However, body size is implicitly embedded in the model because body size tends to increase with trophic level within the community (Jennings et al.

2001). The body-size assumption has been adopted to create simple food web models of gross structure at trophic levels without referring to body size (McCann et al. 2016). For the model used in this study, the 2 alternative BH strategies perform better in terms of total yield and community structure than selectively harvesting fish at high trophic levels or nonselective fishing. In addition, BH can maintain all species co-existence and does not drive one species to extinction before others. Unfortunately, BH performs more poorly than selectively harvesting fish at the bottom of the trophic pyramid in term of maintaining structure. Between the 2 alternative BH strategies, it is hard to determine which one is better in terms of yield and structure. However, from an implementation perspective, BH1 appears to be simpler than BH2 because species productivity is linked to life-history parameters (Zhou et al. 2012), which are easier to obtain than estimating current production used for BH2.

Our results imply trade-offs among maximizing fishery yield and maintaining trophic structure. The trade-offs must also be true for profits to the fishing industry, assuming that fish price depends on trophic level. Selectively harvesting higher trophic levels is a poor strategy for fishery yield, trophic structure, and total biomass with the same amount of catch. Nonselective fishing is also a poor strategy as it causes severe damage to structure. Selectively harvesting the lowest trophic level could possibly maintain trophic structure and produce high yield, however, it is conceivable that the profit may be too low. This may leave BH as a favorable, although not ideal, strategy among the alternatives.

The general conclusions from this study are comparable with other studies using different modeling approaches, although other studies have not specifically evaluated such a wide range of fishing scenarios. Bundy et al. (2005) used an Ecopath model for the Gulf of Thailand ecosystem and the eastern Scotian Shelf ecosystem to explore the effect of fishing pattern on trophic structure. They used an exploitation index (E) similar to our BH2, i.e. the total yield divided by total production for all exploited species. Their results indicate that equal exploitation across the system (similar to BH2) always results in less disturbance than exploitation only at higher trophic levels (similar to our Cases 1 and 2). The Ecopath model also suggests that concentrated fishing on lower trophic levels (similar to our Case 3) has a lower impact on ecosystem structure for any given exploitation rate than for exploitation at higher trophic levels or balanced exploitation.

Law et al. (2012) tested effects of BH against more traditional exploitation strategies using a model of a single fish species with a dynamic size spectrum. Their results show that harvesting smaller fish allows a greater sustainable biomass yield than harvesting larger fish. Balanced exploitation (similar to our BH2) brings fishing mortality more in line with the natural variation in productivity. In addition, the resilience of the ecosystem to perturbations can be improved, and disruption to the size distribution of organisms in the ecosystem reduced. If small fish represent our low trophic level and large fish belong to high trophic levels, the conclusions from size-based models are comparable with ours.

Houle et al. (2013) also used a size-based model to identify management trade-offs among a forage (low trophic level) fishery, a fishery for intermediate predators, and a predator fishery. Their work shows that harvesting predator species enhances the forage fishery yield due to reduced predation mortality on forage fishes. This is comparable to our Case 2 where fishing at TL2 increases prey biomass at TL1. They found that it was not possible to simultaneously maximize yield of forage fishes, intermediate predators, and upper predators; forage fish yield is highest when all larger fishes are essentially eradicated, while fishing at levels that maximize intermediate and upper predator yield results in much lower forage fishery yield. Our scenarios (non-selective fishing, BH1, and BH2) give similar interpretations. In addition, our study evaluates not only yield, but also trophic structure and overall biomass.

It would be interesting to compare our model results with similarly simple traditional Lotka-Volterra models, i.e. a fully coupled system where a predator's growth rate is entirely and exactly determined by its intake rate of prey. There is a series of papers using such models to explore the effect of MSY policy on species extinction (Kar 2003, Legovi 2008, Legovi et al. 2010, Kar & Ghosh 2012, 2013, Ghosh & Kar 2013b, 2014, Ghosh et al. 2014). These studies typically use an analytical approach (i.e. mathematically deriving equilibrium points simultaneously from prey and predator population equations) and apply the Lotka-Volterra model to a single prey and single predator system (2 trophic levels). Although the objectives in these studies (focusing on MSY policy) and the number of trophic levels considered differ from ours, some conclusions from such traditional models may be of interest. For example, it is concluded that in any such prey–predator system, fishing on the prey population only to reach MSY, or fishing on both prey and predator together, will cause extinction of the predator population but not the prey itself. By selectively fishing on predators it is possible to maintain species co-existence, but this reduces predator abundance while increasing prey abundance. Selectively fishing on prey has no effect on prey itself until the predator becomes extinct, because fishing mortality simply replaces predation mortality. These outcomes are theoretically valid for such models, but may be difficult to understand for biologists and fisheries managers.

This study is part of an ongoing exploration, by many authors, of the possible fishery and ecosystem consequences of different patterns of fishing across an ecosystem, using models to explore the dynamics. Walters et al. (2016) remind us that the structural assumptions in these models can be critical to the predictions, and variations to the particular form of the model we used could well result in different predictions and conclusions. Walters et al. (2016) also demonstrated the potential utility of simple models to explore the ecosystem impacts of fishing, and to better understand the dynamics and predictions of more complex models, not least because sensitivity to assumptions can be explored more comprehensively using simple models. As suggested by Garcia et al. (2014) and others, continued research on the ecosystem effects of fishing should involve a range of types of models, including various forms of simple models such as the one used in this study, coupled with attempts to relate model predictions to observed patterns in nature.

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