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The consequences of balanced harvesting of fish communities

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Balanced harvesting, where species or individuals are exploited in accordance with their productivity, has been proposed as a way to minimize the effects of fishing on marine fish communities and ecosystems. This calls for a thorough examination of the consequences balanced harvesting has on fish community structure and yield. We use a size- and trait-based model that resolves individual interactions through competition and predation to compare balanced harvesting with traditional selective harvesting, which protects juvenile fish from fishing. Four different exploitation patterns, generated by combining selective or unselective harvesting with balanced or unbalanced fishing, are compared. We find that unselective balanced fishing, where individuals are exploited in proportion to their productivity, produces a slightly larger total maximum sustainable yield than the other exploitation patterns and, for a given yield, the least change in the relative biomass composition of the fish community. Because fishing reduces competition, predation and cannibalism within the community, the total maximum sustainable yield is achieved at high exploitation rates. The yield from unselective balanced fishing is dominated by small individuals, whereas selective fishing produces a much higher proportion of large individuals in the yield. Although unselective balanced fishing is predicted to produce the highest total maximum sustainable yield and the lowest impact on trophic structure, it is effectively a fishery predominantly targeting small forage fish.

1. Introduction

The ecosystem approach to fishing has increased the interest in managing fisheries impacts at the level of fish communities and ecosystems [1,2], but so far, it is unclear exactly how this can be done. This relates not only to the proper definition and use of the concept of maximum sustainable yield (MSY) in a multi-species management context [2], but also to how exploitation patterns might be changed to better achieve fisheries and conservation objectives simultaneously. Recently, it has been suggested that both objectives can be achieved if species and individuals are exploited in relation to their natural productivity, the so-called balanced harvesting [3,4].

The theoretic rationale behind balanced harvesting is inspired by classic 'surplus production' theory, which predicts that the fishing mortality leading to MSY is proportional to natural mortality [5–7]. In an unexploited situation, natural mortality is equal to production per unit of biomass [8], and it is therefore expected to scale to body mass raised to the power of -0.25 [9]. The natural conclusion is that the largest yield from an ecosystem can be achieved if all species are fished proportional to their theoretical productivity, and hence that small species should be fished more intensely than large species. However, there are two complicating issues: first, most fish have large size differences between offspring and adults, and it is therefore relevant to ask whether productivity is measured at the stock level (as in classic surplus production theory) or at the level of individuals (as in [10,11]). Current single-species MSY management strives to enforce fishing mortality and size selectivity to maximize production in a manner that may be termed 'balanced selective' fishing, where juvenile fish are protected from fishing and adults are fished in proportion to their productivity. An exploitation pattern where each individual is exploited in proportion to its productivity challenges the

predominant belief among fisheries scientists that MSY is achieved when juveniles are protected [12,13]. Second, changes in the abundance at higher trophic levels affect the productivity of lower trophic levels: when the fishing mortality on one trophic level goes up, the predation mortality on the lower trophic level goes down, and consequently that trophic level may tolerate a higher fishing mortality. This replacement of natural mortality by fishing mortality was actually one of the rationales behind balanced harvesting [14], and has the consequence that the fishing mortality producing MSY is different in the multi-species and single-species cases [15]. An evaluation of balanced versus unbalanced harvesting therefore requires a community perspective where changes in trophic interactions owing to fishing are fully accounted for [11].

A central piece of empirical evidence supporting balanced harvesting consists of studies of fisheries along African lakes demonstrating that non-regulated fisheries predominantly targeting smaller individuals had little impact on the size structure of the local fish communities [14,16]. Apart from these studies, the impact of balanced harvesting has mainly been explored through model predictions. Simulations with Ecosim models have shown that increasing the exploitation rate of small species generates less change in biomass distribution across trophic levels than increasing exploitation rate equally across species [17]. Garcia *et al.* [3] compiled results from a series of Ecosim and ATLANTIS models, and concluded that unselective harvesting was superior to selectively fishing fewer ecosystem components. The unselective pattern was better in terms of total yield and biomass, and produced fewer local population extinctions. Many of the models used in these simulations did not resolve the size structure of the species or did so using only few life stages and assuming food-independent growth from one stage to the next. It can therefore be questioned how well these simulations reflect the outcome of unselective harvesting.

Simulations of unselective balanced harvesting, where each individual is fished in proportion to its productivity, require a finely resolved or continuous size structure. Such simulations have only been performed with single-species size-spectrum models where it was found that targeting only small individuals caused less disruption to the size spectrum than targeting larger individuals, and that fishing according to productivity resulted in higher resilience [10,11]. Because unselective balanced harvesting implies a higher fishing intensity on small than on large individuals, we expect the size composition of the catch to differ from that of the traditional size-selective fisheries. A catch composed largely of small individuals may be desirable (e.g. as in some artisanal fisheries [14]), while it may be less so in industrial fisheries for human consumption, where larger individuals, regardless of species, typically return a higher price per weight. It is therefore relevant to extend the description of balanced harvesting beyond total yield and total biomass [3,10,18].

Our aim is to systematically examine how exploitation affects catch and community structure by comparing balanced versus unbalanced and selective versus unselective exploitation patterns. To this end, we use a size-based fish community model that fills the gap between the single-species size spectra and the community models [19–21]. The model provides a mechanistically based description of fish community dynamics, taking account of both intra- and interspecific competition and predation. Compared with traditional single-species models,
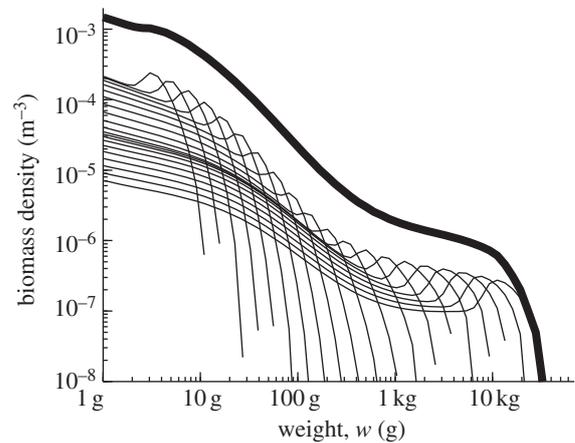

Figure 1. The fish biomass density spectrum in the unfished state. The thick line is the community spectrum, and the thin black lines show 20 'species' with different asymptotic body weights.

predator–prey interactions and food-dependent growth are fully resolved, making the model suitable for long-term projections of an entire community. In contrast to previous publications on balanced harvesting, our model resolves the full life history of the individual fish from egg to adult. These attributes allow to us to explore community responses of exploitation of varying sizes and species in much greater resolution than previously carried out.

To precisely define the terms balanced/unbalanced and selective/unselective fishing, we use four exploitation patterns and use these to address total yield, size composition of yield and biomass distribution at the community level. The patterns differ with respect to whether or not fishing mortality is scaled with productivity (balanced or unbalanced), and whether or not juveniles are protected (selective and unselective). We thus compare the outcome of: (i) *selective unbalanced* fishing, a pattern that is a good approximation to the current exploitation of the North Sea fishes, where juveniles are protected and adults are fished with approximately equal mortality across groups [22]; (ii) *unselective unbalanced* fishing, where all individuals are exploited with the same fishing mortality irrespective of whether they are juveniles or adults; (iii) *selective balanced* fishing, where juveniles are protected from fishing and adult fishing mortality scales with productivity at the population level; and (iv) *unselective balanced* fishing, which is the 'ideal' balanced pattern where each individual is exploited relative to its productivity. For a given total yield, we ask which exploitation pattern results in less change in the distribution of biomass across the community. We also compare the size composition of the catch and show that although balanced fishing causes less change in the structure of the community, it generates a substantial reduction in the average size of fish being caught.

2. Methods

(a) Trait-based size-spectrum model

We use the size-spectrum model developed by Andersen & Beyer [19] to estimate the equilibrium yield and biomass for each of the four exploitation patterns at different levels of fishing. The model is based on individual-level processes—encounters, growth, mortality and reproduction—and represents the fish

Table 1. Equations governing the model. $N_i(w)$ is the abundance density of individual fish with weight w from species i with asymptotic size $W_{\infty i}$.

description	equation	no.
community		
conservation equation	$\dfrac{\partial N_i(w)}{\partial t} + \dfrac{\partial g_i(w)N_i(w)}{\partial w} = -\mu_i(w)N_i(w)$	M1
community spectrum	$N_c(w) = \sum_i N_i(w) + N_R(w)$	M2
food consumption		
lognormal food preference curve	$\phi\left(\dfrac{w_p}{w}\right) = \exp\left[\dfrac{-(\ln(w/(w_p\beta)))^2}{2\sigma^2}\right]$	M3
encounter rate	$E(w) = \gamma w^q \displaystyle\int_0^{\max(W_\infty)} N_c(w)\phi\left(\dfrac{w_p}{w}\right)w\,dw_p$	M4
consumption	$f(w)hw^n = \dfrac{E(w)}{E(w) + hw^n}hw^n$	M5
somatic growth and reproduction		
available energy	$E_a(w) = \alpha f(w)hw^n - k_s w^p$	M6
allocation of energy	$\psi\left(\dfrac{w}{W_\infty}\right) = H\left(\dfrac{\eta_m W_\infty}{w}\right)\left(\dfrac{w}{W_\infty}\right)^{1-n}$	M7
somatic growth	$g_i(w) = E_a(w)\left(1 - \psi\left(\dfrac{w}{W_{\infty,i}}\right)\right)$	M8
egg production	$R_{p.i} = \dfrac{\varepsilon}{2w_0}\displaystyle\int_{w_0}^{W_{\infty,i}} E_a(w)\psi\left(\dfrac{w}{W_{\infty,i}}\right)N_i(w)\,dw$	M9
density dependence	$R = R_{\max.i}\dfrac{R_{p.i}}{R_{p.i} + R_{\max.i}}$	M10
max. recruitment	$R_{\max.i} = \kappa_r(\alpha f_0 hw_0^n - k_s w_0^p)W_{\infty,i}^{2n-q-3+a}(W_{\infty,i} - W_{\infty,i-1})$	M11
mortality		
predation mortality	$\mu_p(w_p) = \displaystyle\int_{w_0}^{\max(W_\infty)} \phi\left(\dfrac{w_p}{w}\right)(1 - f(w))\gamma w^q \sum_i N_i(w)\,dw$	M12
background mortality	$\mu_b = \mu_0 W_\infty^{n-1}$	M13
starvation mortality	$\mu_s(w) = \begin{cases} 0 & \alpha f(w)hq^n > k_s w^p \\ \dfrac{k_s w^p - \alpha f(w)hw^n}{\xi w} & \alpha f(w)hq^n \le k_s w^p \end{cases}$	M14
selective unbalanced fishing	$F(w, W_\infty) = F_0 H\left(\dfrac{w}{\eta_F W_\infty}\right)$	M15
unselective unbalanced fishing	$F = F_0$	M16

(Continued.)

Table 1. (*Continued.*)

description	equation	no.
selective balanced fishing	$F(w, W_\infty) = F_0 \left(\dfrac{W_\infty}{w_m} \right)^{-0.25} H \left(\dfrac{w}{\eta_F W_\infty} \right)$	M17
unselective balanced fishing	$F(w) = F_0 \left(\dfrac{w}{w_m} \right)^{-0.25}$	M18
size-selection function	$H(z) = (1 + z^{-10})^{-1}$	M19
resource spectrum		
resource production	$\dfrac{\mathrm{d}N_R(w)}{\mathrm{d}t} = r_0 w^{p-1}[\kappa w^{-\lambda} - N_R(w)] - \mu_p(w)N_R(w)$	M20

community as a continuum of 'species' with increasing asymptotic body weights. In the computational implementation, the continuum is represented as a discrete number of asymptotic weight classes, which are referred to as 'species' for the sake of simplicity. A species i in the model is characterized by its asymptotic body weight, W_∞, and its population by its size distribution $N_i(w)$. The results from the model are independent of the number of species as long as this is larger than 10. In our simulations, we used 20 species in the range from 10 to 30 000 g (figure 1).

The model rests on two main assumptions: (i) fish eat other fish that are smaller than themselves, and (ii) individual fish can be described exclusively by their individual and asymptotic body weights. The individual-level processes and the scaling from individuals to $N_i(w)$ are described in detail in [21] and summarized in table 1 with parameters defined in table 2. Here, we provide a general overview of the model.

In the model, each individual is described by its asymptotic body weight, W_∞, and by its individual weight, w. Using mechanistically based submodels for growth, mortality and reproduction, the model calculates the number of individuals in each species's weight-group, $N_i(w)$. All processes are subject to a conservation equation (M1), where growth and mortality accounts for the change in the number of fish and biomass within a given size class. In order to grow, an individual must encounter and ingest food. Food is selected from the entire size spectrum (M2) using a lognormal prey size preference (M3). The food encountered by a predator is the product of available food and a size-specific search rate (M4). The amount of encountered food consumed is limited by the maximum rate of food processing hw^n and modelled with a Holling type II functional response (M5).

The food consumed is used on standard metabolism, somatic growth and reproduction. The available energy is what remains after consumption is assimilated and standard metabolism $k_s w^p$ is subtracted (M6). As a mature individual approaches its asymptotic weight, an increasing fraction of the available energy is allocated to reproduction (M7) and this reduces its somatic growth (M8). Growth and reproduction in the model are therefore linked and food-dependent. The particular allocation to reproduction (M7) is chosen such that a constant ratio between consumption and maximum consumption results in a growth pattern similar to a von Bertalanffy curve [21]. When the individual matures, energy is allocated to egg production (M9). Eggs hatch to become larvae using a Beverton–Holt-like density-dependent recruitment function (M10), where the maximum recruitment, $R_{\max,i}$, depends on the equilibrium solution of the model (M11) [19].

Natural mortality comes from three different sources: predation mortality, background mortality and starvation mortality.

Predation mortality is proportional to encounters (M12). Background mortality is implemented to prevent the build-up of large individuals at zero fishing, and is assumed to scale with asymptotic weight (M13). Starvation mortality is only present when feeding is less than required to cover standard metabolism (M14).

To sustain the smallest individuals in the fish community, a dynamic background spectrum of edible plankton is provided. We model the spectrum as a semi-chemostat resource with a carrying capacity determining the total production of the system (M20).

(b) Fishing mortalities

Fishing is imposed as four conceptually different exploitation patterns (figure 2). The patterns differ with respect to their size selectivity within and across species. Further, the exploitation patterns are divided into 'balanced' and 'unbalanced' types of fishing. Selective fishing refers to exploitation patterns where juveniles are protected from fishing and individuals are recruited to the fishery as they approach some fraction of their asymptotic weight. Selection is modelled by a sigmoidal function that switches smoothly from 0 to 1 at the size $\eta_F W_\infty$ (M19). In balanced fishing, individuals or species are exploited in accordance with their productivity as determined by metabolic scaling rules (i.e. scaling fishing mortality with individual or asymptotic body weights with exponent -0.25) [9,25]. Unbalanced fishing allocates F equally over all asymptotic weights or sizes. This gives four different fishing combinations: selective unbalanced fishing, (M15; figure 2a), unselective unbalanced fishing (M16; figure 2b), selective balanced fishing (M17; figure 2c) and unselective balanced fishing (M18; figure 2d). All exploitation patterns are subject to a lower cut-off size where the smallest individuals are recruited to the fishery. Each fishing pattern is scaled with a fishing intensity, F_0. As total fishing mortality at size is a product of selectivity and fishing intensity, comparison of the absolute fishing mortality, F, between the patterns is complicated and should be approached cautiously. To facilitate qualitative comparison, we have nevertheless scaled the fishing intensities such that the fishing mortality of an arbitrary 'medium'-size, fully mature fish weighing $w_m = 444$ g is the same for all exploitation patterns (see dotted lines in figure 2).

We describe the state of the system using three indicators: total yield, spawning stock biomass relative to the unexploited situation and size composition of the yield. The yield in the system is calculated as $Y = \sum_i \int_{w_r}^{W_{\infty,i}} F_i(w)N_i(w)\, w\, \mathrm{d}w$, where w_r is the body size at recruitment to the fishery, and the sum runs over all W_∞ species in the model. We calculate yield and ecosystem state when fishing intensity is gradually increased from 0 to 3 yr^{-1} for each of the four exploitation patterns.

5

Table 2. All parameters in the model.

parameter	value	definition
foraging		
β	100	preferred predator–prey weight ratio [23]
σ	1.3	width of selection curve [20]
γ	29.2 g^{-q} yr^{-1}	search volume factor [21]
q	0.8	search volume exponent [19]
physiology		
h	20 g^{1-n} yr^{-1}	max. consumption factor
n	0.75	max. consumption exponent [20]
η_m	0.25	size at 50% maturation relative to W [20]
α	0.6	assimilation efficiency [20]
κ_s	2.4 g^{1-p} yr^{-1}	standard metabolism factor
p	0.75	standard metabolism exponent [24]
ε	0.1	gonad efficiency [21]
a	0.66	expected mortality/ growth ratio
μ_0	2 g^{1-n} yr^{-1}	background mortality factor
ξ	0.1	fraction of energy reserves used for reproduction
resource		
κ, κ_r	0.005 g$^{\lambda-1}$ m^{-3}	carrying capacity of background spectrum
λ	2.05	resource community exponent
r_0	4 g^{1-p} yr^{-1}	resource community growth factor
fishing		
η_F	0.05	fraction of W_∞ to recruitment for trawl selectivity
w_r	10 g	size at recruitment to fishery
w_m	444 g	size at which $F = F_0$ for all fishing patterns
F_0	free	fishing intensity

3. Results

The largest MSY from the community is generated at a fishing intensity around 1.0 in the unselective balanced fishing scenario, and is approximately 40% higher than the MSY produced by selective balanced harvesting, but only marginally larger than that of the two remaining scenarios (figure 3). These results are fairly robust to change in the lower cut-off size of fishing (see electronic supplementary material). At low fishing mortalities, all exploitation patterns cause trophic cascades owing to the decline in spawning stock biomass of the largest species (figure 4). The trophic cascades make species with an asymptotic weight of approximately 1 kg reach higher spawning stock biomasses than in the unexploited situation, while the largest species collapse (defined as a spawning stock biomass less than 20% of its unexploited value) already at relatively low fishing mortalities, except in the selective balanced fishing scenario where smaller species crash. The community structure generally responds differently to the selective (figure 4a,c) and unselective scenarios (figure 4b,d). Selective fisheries reduce the spawning stock biomass of fish with an asymptotic size around 200 g, most pronounced in the selective balanced harvesting case. For the unselective fisheries, this is less evident. In spite of the amount of species collapsing at the approximate same fishing intensity in all scenarios, further increases in fishing intensity generate a more gradual reduction in biomass in the selective scenarios than in the unselective. The unselective scenarios furthermore exhibit a 'fishing down the food web' type of response, where increasing overall fishing mortality gradually removes species from the large end of the size spectrum.

Considering the relative change in the spawning stock biomass for different species, unselective balanced fishing causes the least change from the unexploited situation at exploitation levels corresponding to 50% and 80% of the largest MSY (figure 5). For the other three types of fisheries, the spawning stock biomasses of the largest species are reduced more. Interestingly, the unselective fisheries do not produce lower total spawning stock biomasses (i.e. spawning stock biomass of all species) than the selective fisheries, even though juveniles are fished. The selective balanced fishery generates very low abundances for some groups at 50% of the largest MSY, and cannot produce 80% of the maximum yield. At the high exploitation rates, the size structure is truncated by all exploitation patterns, with unselective balanced fishing causing the least truncation.

The size composition of the yield depends strongly on the exploitation pattern used (figure 6). At a fishing intensity producing half the largest MSY, selective exploitation produces the highest fraction of large individuals in the yield. Unselective unbalanced fishing also produces approximately the same yield over the 10–1000 g body weight range, but for the larger fish, the yield gradually declines with body weight. The yield from the unselective balanced fishing is dominated by individuals weighing between 10 and 100 g, and few large fish are caught. Increasing the total fishing mortality to produce 80% of the maximum yield provides a similar picture, but with a much reduced yield of large individuals. At the higher fishing mortalities producing 80% of the maximum total yield, the unselective fishery includes only small fish in the catch.

4. Discussion

The simulations show how maximum yield and fish community structure respond to different exploitation patterns. The response is driven by the direct effects of fishing mortality on the exploited populations, and by compensatory changes in
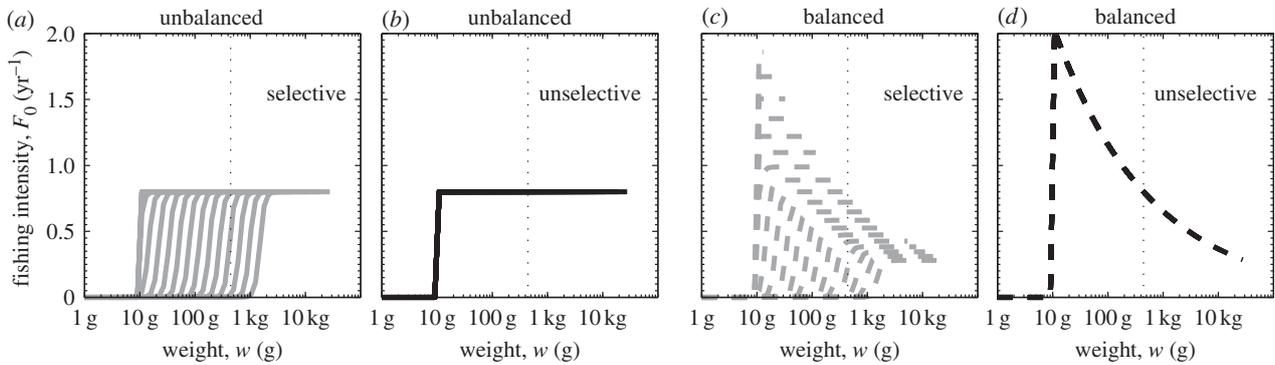
Figure 2. The four different exploitation patterns used in the model with $F_0 = 0.8 \text{ yr}^{-1}$ at a size of 444 g (dotted line). (a,b) The unbalanced exploitation patterns for (a) selective fishing and (b) unselective fishing. (c,d) The two balanced fishing scenarios, for (c) selective and (d) unselective fishing. For all four exploitation patterns, a lower cut-off is imposed at 10 g.
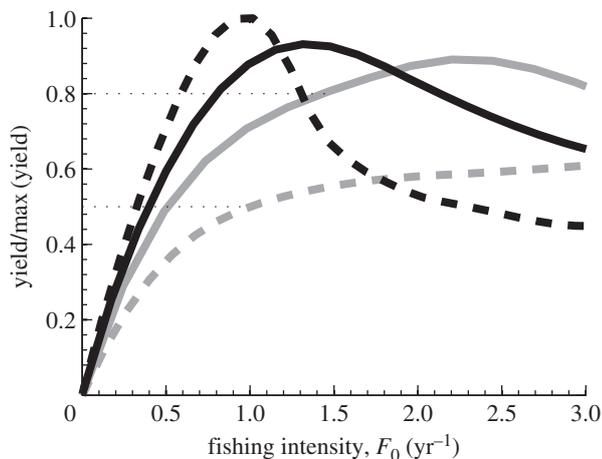

Figure 3. The yield from the four different exploitation patterns. Grey (black) lines are selective (unselective) fishing. Dashed (solid) lines indicate that the fishing is balanced (unbalanced; figure 1). The horizontal dotted lines are 50% and 80% of the maximum yield of the unselected balanced exploitation pattern. The highest total yield is from unselective balanced fishing. The unbalanced fisheries have approximately equal yields, both peaking at high fishing intensities. Selective balanced fishing gives the lowest yield.

growth, recruitment and predation within the community. When fishing reduces the abundance of predators, their prey will suffer less predation mortality. This will, relatively speaking, increase prey abundance and may lead to trophic cascades if the effect spreads across several trophic levels. Such cascades occur in all four scenarios, but are most pronounced when fishing is selective. As the abundance of predators is reduced, the release from predation makes it possible to fish the remaining individuals harder than expected from single-species fish stock assessments, where the fishing mortality producing MSY typically would be around 0.3 yr^{-1} for larger species [26]. Due mainly to reduction in predation mortality, the MSY is generated at much higher levels of fishing mortality, where a high yield is achieved at the expense of a collapse of the largest species.

Traditional single-species fisheries models often predict that fishing on juveniles should be reduced or eliminated in order to better exploit the growth potential of the individuals and thus increase yield [1,12]. Our results show that selective fishing reduces the MSY from the community and does not preserve the distribution of biomass across species as well as unselective fishing. If the management objectives are to

achieve MSY and maintain the unexploited distribution of biomass across species as well as possible, then unselective balanced fishing is more effective than the other fishing strategies (figures 3–5). However, compared with selective unbalanced fishing the yield from unselective balanced fishing is composed of small individuals and species, which may not find as profitable a market as the larger fish caught by selective harvesting (figure 6).

Our results are in line with other recent modelling studies which also predict balanced unselective fishing to generate higher yields than traditional fishing patterns [3,4,27]; however, our analysis reveals that several fishing patterns (including unbalanced fishing) have almost the same maximum yield and that the yield in the balanced case will consist of fairly small fish. In all fishing patterns, low-trophic-level individuals account for a large part of the catch, which explains similarities in total yield. The targeting of small species ('forage fisheries') is in conflict with recent publications where it is argued that small fish species should be exploited at levels well below those producing MSY [28–30]. Those results emerge because exploitation of forage fish species not only affects the species themselves, but also affects top predators such as the seabirds and marine mammals predating upon them [29,31].

One aspect of harvesting that we do not address is to which degree fishing creates or amplifies temporal variability in abundance of fish. Law et al. [10] show that balanced harvesting reduces variability in a single-species context. Community-level simulations have shown that selective fishing increases variability [32]; however, this was done with a model that did not resolve life-history diversity. It has since then been shown that excluding life-history diversity creates artificially high temporal variability [33], so these results should be revisited, preferably in the context of balanced harvesting.

(a) Modelling approach

The model contains the most important biological processes and interactions taking place in a fish community and predicts the consequences of changing its trophic structure. However, like many other fish stock models, it relies on a stock–recruitment function with a weak mechanistic foundation. The function is included to stabilize the model and prevent competitive exclusion [34]. Ecosystem models need one or several controlling processes to generate coexistence of a larger number of species. Specific examples are ratio-dependent functional response [35],
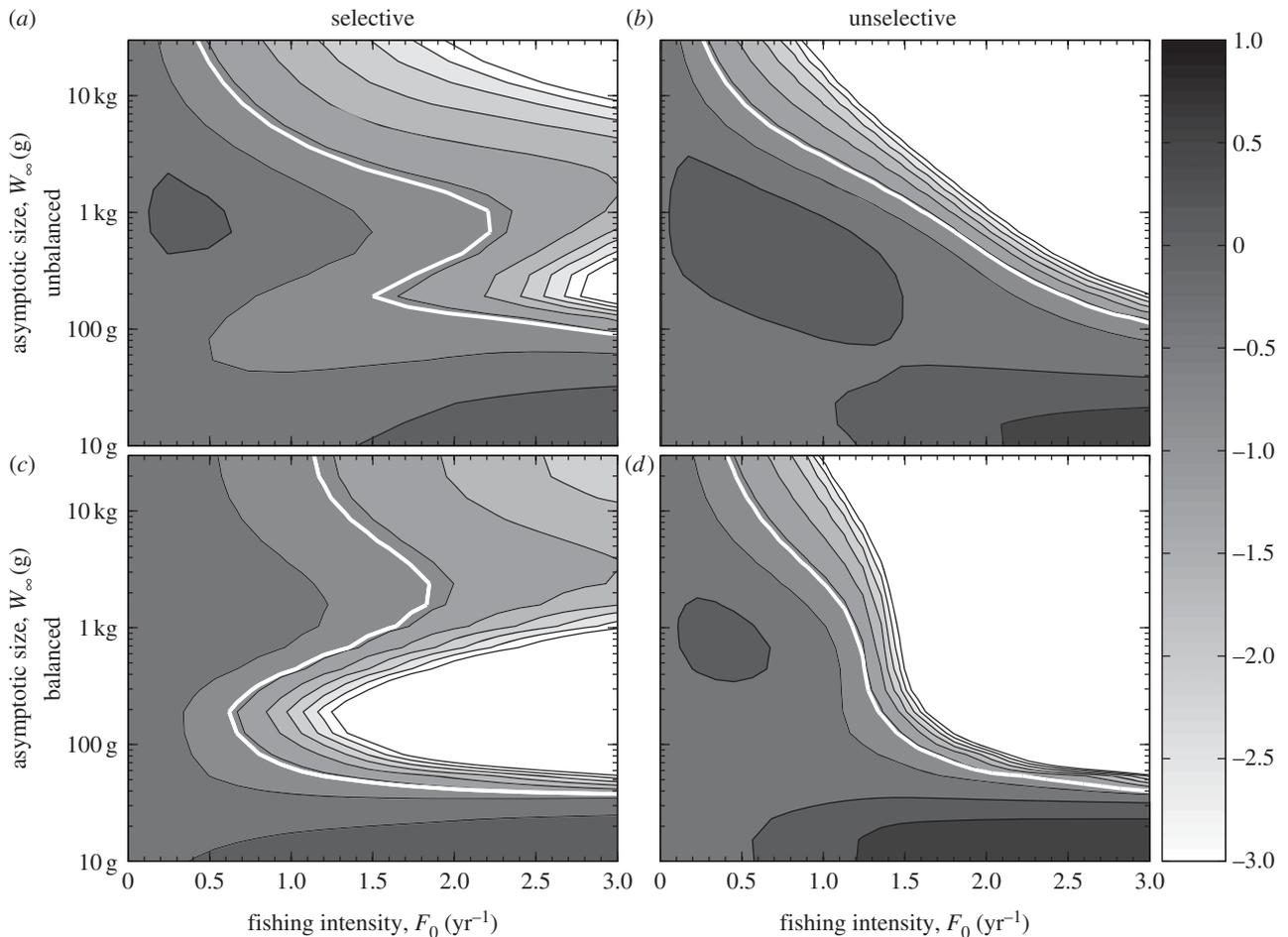
Figure 4. Spawning stock biomass relative to the unfished spawning stock biomass on $\log_{10}$ scale. White lines show 20% of unfished spawning stock biomass. (*a*) Selective unbalanced fishing removes the largest spawners at low fishing mortality, causing their main prey (asymptotic weight range 500 g $< W_\infty <$ 2 kg) to be less impacted by fishing. At high fishing intensities, only the smallest species remain. (*b*) Unselective unbalanced fishing fishes down the entire food web as fishing intensity increases. (*c*) Selective balanced fishing preserves community structure up to about $F_0 \approx 1$ yr^{-1}, where the largest species are removed, causing a cascade through the community; the smallest individuals have a small refuge due to the mesh size used. (*d*) Unselective balanced fishing also fishes down the food web, but with a sharper decline in abundance of large species than the unbalanced fishery.

stock–recruitment relationships [36], prey switching [37] or food webs with more weakly linked components [21,38]. The implemented stock–recruitment relationship is characterized by two things: the slope at the origin that controls the degree of density dependence, and maximum recruitment. The slope at the origin is an emergent property of the model as it is determined by the food-dependent egg production [26]. Maximum recruitment is defined as a declining function of W_∞ (M11), and the specific functional form is determined from the equilibrium solution of the model [19]. This functional form has been independently verified from food-web model simulations, which do not use a stock–recruitment function [21]. The only free parameter is thus the total recruitment in the system κ_r, but the dynamics of the system are fairly insensitive to changes in this parameter [39].

We used metabolic scaling as an indicator of relative productivity in our calculations rather than as a dynamically calculated productivity. Productivity is essentially a rate (dimension = time^{-1}), and specific ways to calculate it have been proposed [25]. Law *et al.* [10] defined productivity at the individual level by making fishing mortality proportional to the somatic growth rate of an unexploited population. Another measure of individual productivity would be to consider the biomass production rate, which depends on consumption and predation mortality [40]. In both cases, productivity is a dynamic property that is difficult to measure in nature because it depends on the density of predators and prey. Theoretically, the unexploited productivity would obey metabolic scaling rules, which we have applied in our simulations.

Our implementation of the Andersen and Beyer model uses parameter values reflecting the life history of an average fish, without differentiating between fast- and slow-growing species, or between species with high and low reproductive output. It is not suited to predict the consequences of fishing on slow-growing, late-maturing species with large offspring size and low fecundity, such as sharks and rays, which are likely to be particularly sensitive to fishing [41]. The model describes the response of fish communities to perturbations and we expect similar responses if the simulated exploitation patterns were applied to concrete species and systems. Further progress is needed in the parametrization of size-structured models to investigate consequences of balanced harvesting in applied management of marine ecosystems.

5. Conclusion

We have applied a trait- and size-based model to assess the impacts of fishing on fish communities and yield. Our results show that unselective balanced harvesting is more likely to
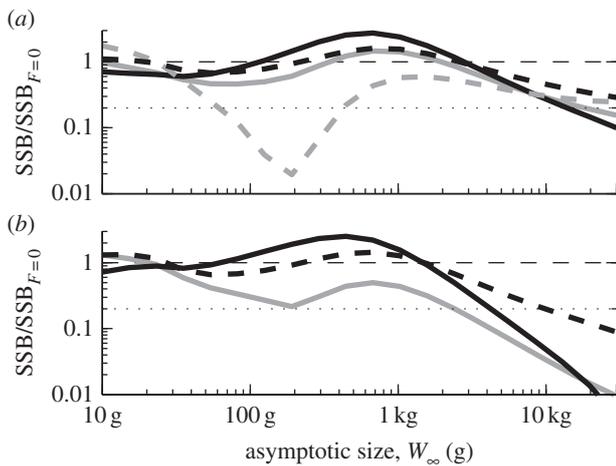
Figure 5. Relative spawning stock biomasses at (a) 50% and (b) 80% of the MSY from the unselective balanced exploitation pattern (see dashed lines in figure 3). Grey (black) lines are selective (unselective) fishing. Dashed (solid) lines indicate that the fishing is balanced (unbalanced; figure 1). The unselective unbalanced fishing (solid black) causes the most severe trophic cascades in the community. The other exploitation patterns also cause some cascades, but they are relatively smaller. Unselective balanced fishing (black dashed) is the only fishery that protects the largest species. For all fisheries, fish with an asymptotic weight in the range 500 – 1000 g have the largest biomass. The selective balanced fishery (grey dashed) does not reach 80% of the maximal yield and does therefore not figure in (b).
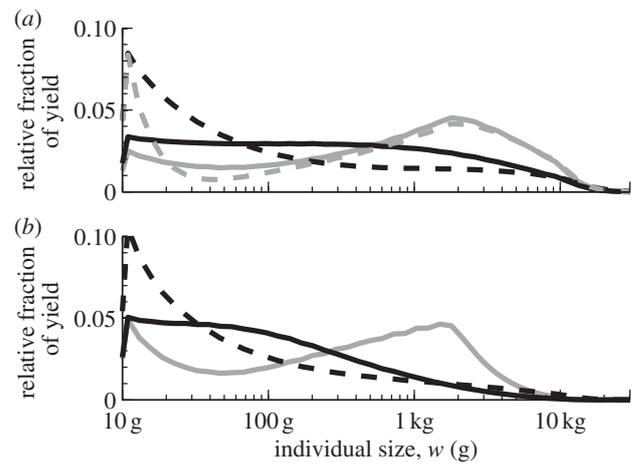
Figure 6. The relative size composition of the yield at (a) 50% and (b) 80% of the MSY from the unselective balanced exploitation pattern. Grey (black) lines are selective (unselective) fishing. Dashed (solid) lines indicate that the fishing is balanced (unbalanced; figure 1). Under moderate fishing pressure (a), the selective unbalanced fishing (solid grey) has the highest fraction of large individuals in the yield ($\approx 1 - 10$ kg), whereas the unselective balanced fishing (dashed black) has the highest fraction of individuals less than 100 g. The unselective unbalanced fishing (solid black) distributes the yield equally over a large size range, but also with few large individuals. The selective balanced fishery (dashed grey) predominantly catches a combination of many small and also some large individuals. At higher exploitation levels (b), the selective unbalanced fishery (solid grey) has the highest fraction of the yield between 100 and 1000 g, but also some individuals at 10 g. The unselective balanced fishing (dashed black) has the same pattern as with lower fishing intensities, with a high proportion of the yield being small fish. The selective balanced fishery does not reach 80% of the maximum yield.

preserve the structure of fish communities than unbalanced fisheries, but with a major reduction in the average size of the fish being caught.

Implementing balanced harvesting in traditional industrial fisheries would require increased targeting of smaller ecosystem components and elimination of current minimum mesh size regulations [42]. The exploitation patterns used in this study reflect fishing mortalities that should be enforced at the management level. The resulting fisheries could, however, turn out to be less profitable in markets where large fish often return a higher price per kilogram than small fish. In many richer countries, the demand for small fish for human consumption is low. In these countries, balanced harvesting may result in a change towards industrial fisheries for production of fish meal and oil or for providing feed to the aquaculture industry, at the same time as the yield of wild caught high value fish for human consumption is reduced. In developing countries dominated by artisanal fisheries, and where consumers are willing to buy and use small fish for human consumption, balanced harvesting may be easier to implement [14].

Although balanced harvesting is an interesting concept, we agree with Maxwell *et al.* [43] when they conclude that its practical implementation and ecological and socio-economic consequences need to be further studied before it can be used as a general principle to guide the rational exploitation of fish communities in the context of ecosystem-based management.

References

1. Pikitch EK *et al.* 2004 Ecosystem-based fishery management. *Science* **305**, 346 – 347. (doi:10.1126/science.1098222)

2. Link JS. 2002 What does ecosystem-based fisheries management mean? *Fisheries* **27**, 18 – 21.

3. Garcia SM *et al.* 2012 Reconsidering the consequences of selective fisheries. *Science* **335**, 1045 – 1047. (doi:10.1126/science.1214594)

4. Zhou S *et al.* 2010 Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *Proc. Natl Acad. Sci. USA* **107**, 9485 – 9489. (doi:10.1073/pnas.0912771107)

5. Caddy JF, Sharp GD. 1986 An ecological framework for marine fishery investigations. *FAO Fisher. Technical Paper* **238**, 152.

6. Francis RC. 1974 Relationship of fishing mortality to natural mortality at the level of maximum sustainable yield under the logistic stock production model. *J. Fish. Board Can.* **31**, 1539 – 1542. (doi:10.1139/f74-189)

7. Zhou S, Yin S, Thorson JT, Smith AD, Fuller M, Walters CJ. 2012 Linking fishing mortality reference points to life history traits: an empirical study. *Can. J. Fish. Aquat. Sci.* **69**, 1292 – 1301. (doi:10.1139/f2012-060)

8. Allen KR. 1971 Relation between production and biomass. *J. Fish. Board Can.* **28**, 1573 – 1581. (doi:10.1139/f71-236)

9

rspb.royalsocietypublishing.org Proc. R. Soc. B 281: 20132701

9. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004 Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789. (doi:10.1890/03-9000)

10. Law R, Plank MJ, Kolding J. 2012 On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES J. Mar. Sci.* **69**, 602–614. (doi:10.1093/icesjms/fss031)

11. Law R, Kolding J, Plank MJ. In press. Squaring the circle: reconciling fishing and conservation of aquatic ecosystems. *Fish Fish.* (doi: 10.1111/faf.12056)

12. Beverton R, Holt S. 1957 On the dynamics of exploited fish populations. *Fish. Invest. Ser. 2* **19**, 1–153.

13. Vasilakopoulos P, O'Neill F, Marshall C. 2012 Differential impacts of exploitation rate and juvenile exploitation on NE Atlantic fish stock dynamics over the past half century. *Fish. Res.* **134–136**, 21–28. (doi:10.1016/j.fishres.2012.08.006)

14. Jul-Larsen E. 2003 *Management, co-management or no management? Major dilemmas in southern African freshwater fisheries 2: case studies*. FAO Fisheries Technical Paper 426/2. Rome, Italy: Food and Agriculture Organization of the United Nations.

15. Gislason H. 1999 Single and multispecies reference points for Baltic fish stocks. *ICES J. Mar. Sci.* **56**, 571–583. (doi:10.1006/jmsc.1999.0492)

16. Kolding J, van Zwieten PAM. 2011 The tragedy of our legacy: how do global management discourses affect small scale fisheries in the south? *Forum Dev. Stud.* **38**, 267–297. (doi:10.1080/08039410.2011.577798)

17. Bundy A, Fanning P, Zwanenburg KCT. 2005 Balancing exploitation and conservation of the eastern Scotian Shelf ecosystem: application of a 4D ecosystem exploitation index. *ICES J. Mar. Sci.* **62**, 503–510. (doi:10.1016/j.icesjms.2004.12.008)

18. Shephard S, Fung T, Houle JE, Farnsworth KD, Reid DG, Rossberg AG. 2012 Size-selective fishing drives species composition in the Celtic Sea. *ICES J. Mar. Sci.* **69**, 223–234. (doi:10.1093/icesjms/fsr200)

19. Andersen KH, Beyer JE. 2006 Asymptotic size determines species abundance in the marine size spectrum. *Am. Nat.* **168**, 54–61. (doi:10.1086/504849)

20. Andersen KH, Pedersen M. 2010 Damped trophic cascades driven by fishing in model marine ecosystems. *Proc. R. Soc. B* **277**, 795–802. (doi:10.1098/rspb.2009.1512)

21. Hartvig M, Andersen KH, Beyer JE. 2011 Food web framework for size-structured populations. *J. Theor. Biol.* **272**, 113–122. (doi:10.1016/j.jtbi.2010.12.006)

22. Pope JG, Rice JC, Daan N, Jennings S, Gislason H. 2006 Modelling an exploited marine fish community with 15 parameters—results from a simple size-based model. *ICES J. Mar. Sci.* **63**, 1029–1044. (doi:10.1016/j.icesjms.2006.04.015)

23. Andersen KP, Ursin E. 1977 A multispecies extension to the Beverton and holt theory of fishing, with accounts of phosphorus circulation and primary production. *Meddr. Danm. Fisk.-og Havunders. N.S.* **7**, 319–343.

24. West GB, Brown JH, Enquist BJ. 1997 A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126. (doi:10.1126/science.276.5309.122)

25. Andersen KH, Farnsworth KD, Pedersen M, Gislason H, Beyer JE. 2009 How community ecology links natural mortality, growth, and production of fish populations. *ICES J. Mar. Sci.* **66**, 1978–1984. (doi:10.1093/icesjms/fsp161)

26. Andersen KH, Beyer JE. In press. Size structure, not metabolic scaling rules, determines fisheries reference points. *Fish Fish.* (doi:10.1111/faf.12042)

27. Rochet M-J, Collie JS, Jennings S, Hall SJ. 2011 Does selective fishing conserve community biodiversity? Predictions from a length-based multispecies model. *Can. J. Fish. Aquat. Sci.* **68**, 469–486. (doi:10.1139/F10-159)

28. Smith AD *et al.* 2011 Impacts of fishing low-trophic level species on marine ecosystems. *Science* **333**, 1147–1150. (doi:10.1126/science.1209395)

29. Pikitch EK *et al.* In press. The global contribution of forage fish to marine fisheries and ecosystems. *Fish Fish.* 1–22. (doi:10.1111/faf.12004)

30. Kaplan IC, Brown CJ, Fulton EA, Gray IA, Field JC, Smith ADM. 2013 Impacts of depleting forage species in the California current. *Environ. Conserv.* **40**, 380–393.

31. Cury PM *et al.* 2011 Global seabird response to forage fish depletion: one-third for the birds. *Science* **334**, 1703–1706. (doi:10.1126/science.1212928)

32. Rochet M-J, Benoît E. 2012 Fishing destabilizes the biomass flow in the marine size spectrum. *Proc. R. Soc. B* **279**, 284–292. (doi:10.1098/rspb.2011.0893)

33. Zhang L, Thygesen UH, Knudsen K, Andersen KH. 2013 Trait diversity promotes stability of community dynamics. *Theor. Ecol.* **6**, 57–69. (doi:10.1007/s12080-012-0160-6)

34. Hartvig M, Andersen KH. 2013 Coexistence of structured populations with size-based prey selection. *Theor. Popul. Biol.* **89**, 24–33. (doi:10.1016/j.tpb.2013.07.003)

35. Christensen V, Walters CJ. 2004 Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.* **172**, 109–139. (doi:10.1016/j.ecolmodel.2003.09.003)

36. Hall SJ, Collie JS, Duplisea DE, Jennings S, Bravington M, Link J. 2006 A length-based multispecies model for evaluating community responses to fishing. *Can. J. Fish. Aquat. Sci.* **63**, 1344–1359. (doi:10.1139/f06-039)

37. Maury O, Poggiale J-C. 2013 From individuals to populations to communities: a dynamic energy budget model of marine ecosystem size-spectrum including life history diversity. *J. Theor. Biol.* **324**, 52–71. (doi:10.1016/j.jtbi.2013.01.018)

38. Rossberg AG, Houle JE, Hyder K. 2013 Stock–recruitment relations controlled by feeding interactions alone. *Can. J. Fish. Aquat. Sci.* **70**, 1438–1446. (doi:10.1139/cjfas-2012-0531)

39. Houle J, Andersen KH, Farnsworth K, Reid D. 2013 Emerging asymmetric interactions between forage and predator fisheries impose management trade-offs. *J. Fish Biol.* **83**, 890–904.

40. De Roos AM, Metz JA, Persson L. 2013 Ontogenetic symmetry and asymmetry in energetics. *J. Math. Biol.* **66**, 889–914. (doi:10.1007/s00285-012-0583-0)

41. Stevens J, Bonfil R, Dulvy N, Walker P. 2000 The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES J. Mar. Sci.* **57**, 476–494. (doi:10.1006/jmsc.2000.0724)

42. Brewer D, Heales D, Milton D, Dell Q, Fry G, Venables B, Jones P. 2006 The impact of turtle excluder devices and bycatch reduction devices on diverse tropical marine communities in Australia's northern prawn trawl fishery. *Fish. Res.* **81**, 176–188. (doi:10.1016/j.fishres.2006.07.009)

43. Maxwell SM, Hazen EL, Morgan LE, Bailey H, Lewison R. 2012 Finding balance in fisheries management. *Science* **336**, 413. (doi:10.1126/science.336.6080.413-a)