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Balanced harvesting can emerge from fishing decisions by individual fishers in a small-scale fishery

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Balanced harvesting can emerge from fishing decisions by individual fishers in a small-scale fishery

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Abstract

Catching fish in proportion to their productivity, termed balanced harvesting, has been suggested as a basis for the ecosystem approach to fishing. Balanced harvesting has been criticised as uneconomical and unachievable because of the level of micromanagement it would require. Here, we investigate the consequences of allowing a fixed number of fishers in a small-scale fishery to choose what size fish to attempt to catch. We examine this from a game-theoretic perspective and test our predictions using an agent-based model for fishers' decisions coupled with a size-spectrum model for the dynamics of a single fish species. We show that small-scale gillnet fishers, operating without size-based regulations, would end up catching small and large fish in proportion to their productivity, in other words balanced harvesting. This is significant because it shows that, far from being unachievable, balanced harvesting can emerge without external intervention under some circumstances. Controls are needed to prevent overfishing, but minimum size regulations alone are not sufficient to achieve this, and actually reduce the sustainable yield by confining fishing to a relatively unproductive part of the size spectrum. Our findings are particularly relevant for small-scale fisheries in areas where there is poverty and malnutrition because here provision of biomass for food is more important than the market value of the catch.

Keywords: balanced harvesting; ideal free distribution; Nash equilibrium; productivity; size spectrum; small-scale fisheries.

Introduction

Balanced harvesting (Garcia et al., 2012, 2015b) has recently been developed as a systematic basis for the ecosystem approach to fishing (Misund et al., 2002, Zhou et al., 2010; Garcia et al., 2015a). The idea is to distribute a moderate fishing mortality across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural productivity, so that the relative size and species composition is maintained (Garcia et al., 2012). The response to this idea has been sensibly cautious, as there is much to learn about how it impinges on aquatic ecosystems and the fishing industry (Burgess et al. 2015). Froese et al. (2015) argued that balanced harvesting (BH) could not be implemented, a view supported by Andersen et al. (2016). Reid et al. (2016) argued that BH would require an impractical level of micro-management. Howell et al. (2016) also raised important questions about the implementation of BH and what benefits might accrue if it is only possible to achieve something less than perfect BH.

The purpose of this paper is to respond to the criticisms about implementation of BH by showing that it can emerge **in a small-scale fishery** from individual fishers working imperfectly and inefficiently towards maximising their own biomass yields. Put another way, the behaviour of fishers themselves can generate BH, in the absence of external controls. There are of course constraints on this. First, our argument is about biomass yield in inefficient, small-scale, artisanal fisheries, not about market value of the catch in major industrial fisheries of the developed world. **Small-scale fisheries employ about 90% of the world's fishers and generate at least 70% of the global catch for human consumption (Kolding and van Zwieten, 2011; Mills et al., 2011).** Second, it is an argument about how fishing becomes distributed over body sizes of fish: it does not solve problems about total fishing effort that could lead to destruction of the resource. Third, there is no suggestion here that the yield from the ecosystem, aggregated over fishers, is at a global maximum when BH emerges. Fourth, we demonstrate the result in a simple, single-species, size-structured ecological model. Fifth, there is no claim that all behavioural decisions made by fishers lead to BH: the limits on fisher behaviour that allow this is also important for future work. **Finally, our results are calculated at equilibrium, whereas real systems frequently do not operate at equilibrium due to numerous factors including environmental variability.** Despite these caveats, given the prevailing view that BH cannot be implemented without detailed biological information and micro-management, we think it is important to be aware that BH can emerge in the absence of external controls. **Understanding how BH can emerge in a small-scale fishery is an important precursor to investigating it a larger-scale, commercial setting.**

How fishers choose the size of fish to target can be viewed as a game-theoretic question because the size-structure of the stock, and therefore the return to a fisher targeting a given size, is affected by the actions of the other fishers. The use of game theory in fisheries management originated with the seminal paper of Munro (1979). Most subsequent work in this area has focused on decisions of multiple players about effort levels, and the conditions necessary for cooperation and avoidance of overfishing (Sumaila, 1999; Bailey et al., 2010). The literature on behavioural models of fleet dynamics has demonstrated that accounting for human behaviour is a key element in effective fisheries management (Branch et al., 2006; Fulton et al., 2011; Milner-Gulland, 2011). However, models of fleet dynamics focus mainly on decisions about effort level, the distribution of effort over space, compliance, discarding and/or investment strategy (van Putten et al., 2012). Here, we are interested in individual fishers' decisions about what size fish to target, in a fixed-effort context, and how these decisions aggregate to produce a distribution of fishing mortality over body size. To our knowledge, this is the first modelling study to address this issue.

Our argument is in two steps. First we show that fishers' behaviour in a **small-scale fishery** leads them to a Nash equilibrium at which the stock biomass is constant over the exploited range of body sizes and each individual fisher obtains the same biomass catch. This state resembles the ideal free distribution in predator-prey interactions, in which the number of predators at a given location is proportional to the rate at which prey are produced at that location, and all individual predators obtain the same prey intake rate (Kacelnik et al., 1992). The ideal free distribution has also been used as a conceptual model for the spatial distribution of fishing effort and predicts that fishing effort will be distributed over space in such a way as to equalize the catch per unit effort among all spatial locations (Gillis et al., 1993; Gillis and van der Lee, 2012). Our model gives an analogous prediction for the distribution of fishing over body size: that catch per unit effort is the same at all exploited body sizes and that fishing effort is proportional to the rate of biomass production across body sizes.

The predictions stemming from the Nash equilibrium are independent of any specific ecological model describing the dynamics of the ecosystem. Since the Nash equilibrium is an idealised limiting case, our second step is to embed the fisher dynamics into a simple ecological model. This shows that the fishing mortality rate, aggregated over fishers, is close to proportional to productivity. In other words, the behaviour of the fishers, coupled to the ecological dynamics generates BH.

We test our theoretical predictions using an agent-based model for fishers' choice of target fish size coupled with a size-spectrum model (Law et al., 2015b) for the dynamics of a single fish species. **In size-spectrum models, fish only grow by eating other organisms (Benoît and Rochet, 2004; Andersen and Beyer, 2006; Law et al., 2009) and, in the single-species version of the model of Law et al. (2015b), the only food sources are a fixed resource**

spectrum and smaller conspecifics. This means that density dependence operates throughout life via predation, rather than being confined to specific life stages, for example through a stock-recruitment relationship (Andersen et al., 2016). The fixed resource spectrum also means that there is no competition for food in the early life stages. Alternative assumptions behind size-spectrum models are the subject of ongoing debate (Froese et al., 2015; Andersen et al., 2016; Froese et al., 2016a). However, the key result we present in this paper is robust to model selection and is not dependent on the specific assumptions of the model of Law et al. (2015b). The agent-based model for fishers' behaviour provides significant novelty relative to Law et al. (2015b), which effectively assumed complete knowledge of the productivity-at-size in order to specify the fishing mortality, whereas here fishers have no knowledge of productivity.

Although most fisheries operate in a multi-species ecosystem, and there is growing call for ecosystem-based fisheries management (Zhou et al., 2010; Garcia et al., 2015a), we use a single-species model because our aim is to understand the mechanisms determining emergent, system-level patterns with respect to body size arising from individual fishers' choices. This is best approached in a single-species framework initially, so that body size is the only independent variable and the results are not confounded by differing species traits and catchabilities. Extending this to a multi-species model is a priority for future work.

Real-world aquatic ecosystems in which to examine these ideas are hard to find because almost all fisheries are subject to external controls (Misund et al., 2002). We present data from the **small-scale fishery** in the isolated Bangweulu Swamps of Northern Zambia as a rare exception to this rule. These multi-species catch data are not directly comparable with our single-species model and not intended as model validation. Nevertheless, we find that the aggregated catch, which has been sustained for many years, encompasses a wide range from very small to large fish, consistent with a Nash equilibrium. These data are contrasted with the catch from a major commercial fishery in the Celtic Sea.

Methods

Size-spectrum model for the ecological dynamics

We use a dynamic size-spectrum model (Law et al., 2015b and Supporting Information, section 1) for a single fish species living together with a fixed resource spectrum. The core of the model is the McKendrick–von Foerster equation for a size-structured population:

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial x}(\varepsilon g u) - (\mu + F)u, \tag{1}$$

This equation is used to calculate the abundance $u(x,t)$ of fish with log body mass $x = \ln(w/w_0)$ at time t, where w is body mass and w_0 is the mass of an egg. In Eq. (1), $g(x,t)$ and $\mu(x,t)$ and are the mass-specific food intake rate and the natural mortality rate at log body mass x. $F(x,t)$ is the fishing mortality rate, which is calculated from the agent-based fishing model (see below). The rates $g(x,t)$ and $\mu(x,t)$ are calculated as functions of the abundance of potential prey and predators, respectively:

$$g(x,t) = AKe^{(\alpha-1)x}\int e^{x'}s(x-x')\,(u(x',t)+u_r(x'))dx', \tag{2}$$

$$\mu(x,t) = A\int e^{\alpha x'}s(x'-x)u(x',t)dx' + \mu_o(x,t). \tag{3}$$

In this model, the volume searched by a predator of log body mass x per unit time is $Ae^{\alpha x}$, which increases allometrically with body mass. Predation rates are a Gaussian function s of the log predator:prey body mass ratio, with mean β and variance σ^2. The function $u_r(x)$ represents a fixed resource spectrum, which provides a food source for small fish (Eq. S5). The function $\mu_o(x,t)$ represents intrinsic, non-predation mortality that increases when the food intake rate $g(x,t)$ is low (Eq. S6). A fixed proportion K of consumed prey biomass is assimilated into predator tissue, of which a proportion $\varepsilon(x)$ is used for somatic growth and $1-\varepsilon(x)$ is used for reproduction. The reproduction function $\varepsilon(x)$ is equal to 1 for small fish and decreases to 0 at the asymptotic log body mass $x_\infty = \ln(w_\infty/w_0)$ (Eq. S7). All offspring have the same initial body mass w_0 and the abundance at size w_0 is determined by the population reproduction rate (Eq. S8). **In contrast to other size-spectrum models (Jacobsen et al., 2014), we do not assume a stock-recruitment function; instead all reproductive output is converted into viable eggs. However, the proportion of these eggs that survive to a given size depends on the abundance of prey, which determines how quickly they grow, and the abundance of predators, which determines how likely they are to die. Recruitment to a given size can therefore be calculated as a model output. The emergent relationship between spawning stock biomass and recruitment can be plotted and results in a familiar density-dependent curve (Fig. S2). We are investigating equilibrium behaviour and the model does not include environmental variability that can lead to large year-to-year variations in recruitment (Sparre and Venema, 1998), i.e. we are modelling stable recruitment (though see Supporting Information, section 2 for effects of variable recruitment).**

The model is built around an explicit bookkeeping of biomass transfer as a result of predation (Law et al., 2015a): predators cannot grow or reproduce without eating prey. As a result, the size-spectrum model internalises feedbacks on the growth, reproduction and mortality rates that must be externally specified in other approaches such as yield-per-recruit (YPR) models. Although small fish can grow to a certain size by feeding on the fixed resource spectrum, they cannot grow towards asymptotic sizes without consuming smaller fish**, which in the case of a single-species model means cannibalism**. If prey become depleted, for example by fishing or by depletion of adult spawners, their predators will experience slower growth (Eq. 2) and increased starvation mortality (Eq. S6). Conversely, if predators become depleted, their prey experience a release from predation mortality (Eq. 3). For a full derivation of the size-spectrum model, see Law et al. (2015b). We parameterise the size-spectrum model to represent African catfish (*Clarias gariepinus*), one of the most commercially important freshwater fish species in Africa. Parameter values are given in Table 1. **African catfish is a relatively fast-growing species (see Fig. S1 for comparison with von Bertalanffy growth model) and this means that it can support higher fishing mortalities than slower-growing species.**

Agent-based fishing model

We develop an agent-based model to simulate the size selectivity of a fixed number N_F of fishers using gillnets. We assume that the ith fisher contributes a fishing mortality $F_i(x)$ that is a Gaussian function of log body mass with mean $x_{f,i}$, fixed standard deviation $\sigma_F = 0.1$ and area under curve equal to F_0:

$$F_i(x) = \frac{F_0}{\sigma_F\sqrt{2\pi}} \exp\left(-\frac{\left(x - x_{f,i}\right)^2}{2\sigma_F^2}\right) \tag{4}$$

This amounts to assuming that each individual fishes with the same constant effort; the only decision made by the fisher is the log body mass $x_{f,i}$ to be targeted. This is a simplification as it ignores changes in individual effort and changes in the number of fishers that might occur as a result of variable yields, but is directly comparable to standard fisheries models in which the fishing mortality F is specified as a model parameter. The Gaussian function is equivalent to the log-normal size selectivity curves estimated from experimental gillnet catches in a small-scale fishery in Lake Kariba (Kolding et al., 2016a) and an individual fisher's choice of $x_{f,i}$ corresponds to a choice of mesh size. The aggregate fishing mortality $F(x)$ is simply the sum of the N_F individual fishing mortality functions:

$$F(x) = \sum_{i=1}^{N_F} F_i(x). \tag{5}$$

This defines the $F(x)$ that is used in Eq. (1). **The key difference from standard fisheries models is that the effective size selectivity of the fishery as a whole is not an externally specified function, but an emergent outcome of individual agents' behaviour.** The biomass catch $Y_i(t)$ of the ith fisher at time t is calculated from the size-spectrum model as an integral over body mass of the mortality rate for that fisher multiplied by the biomass density, which is the product of abundance $u(x,t)$ and body mass $w_0 e^x$:

$$Y_i(t) = w_0 \int_0^{x_\infty} F_i(x)\, u(x,t) e^x dx \tag{6}$$

After every time period T_F, the ith fisher has a probability $q_i = 1 - Y_i(t)/Y_{\max}(t)$ of switching to a new target body mass, where $Y_{\max}(t)$ is the highest catch of all individual fishers at time t. Hence, the fisher with the largest catch at time t will continue with the same target size; fishers with lower catches are increasingly likely to switch to a new target size. The new target log body mass $x_{f,i}$ is chosen randomly from a uniform distribution on $[0, x_\infty]$ (or $[x_{Fmin}, x_\infty]$ when a minimum target size regulation x_{Fmin} is imposed). Thus a fisher's choice of target size is always completely random, but if he/she happen to choose a target size that gives a relatively large catch, he/she is more likely to continue with that target size. However, if a fisher's catch subsequently drops, for example if lots of fishers target the same size causing depletion of fish around that size and hence reduced catches, then they will become more likely to try a different target size.

This is clearly an oversimplified model that ignores a wide range of factors that could influence fisher's decisions about target size, for example: knowledge of other fishers' target sizes or the current size structure of the stock; memory of previous catches; costs associated with changing target size; cooperation or any behaviour that is not strictly rational (Fulton et al., 2011; van Putten et al., 2012). However, the model is not intended to realistically simulate individual fisher's decisions; rather, we are interested in the aggregate fishing pattern that emerges from this this very simple rule set at the individual level. This "complexity from simplicity" approach is the classic use of agent-based modelling (Bonabeau, 2002), for example the Schelling (1971) model of ethnic segregation and exemplified by Axelrod (1997) advocating the "Keep it simple, stupid" (KISS) principle. The aim is to learn about how simple mechanisms can potentially lead to emergent phenomena, rather than to simulate realistic human behaviour. **This agent-based model could readily be applied to other models for the ecological dynamics of the stock.**

Simulation method

At the beginning of the simulation, the size spectrum is initialised in the steady state of the model with constant fishing mortality applied at all body masses. The individual fishers have initial target log body masses $x_{f,i}$ drawn independently from a uniform distribution on $[0, x_\infty]$. The long-term output of the model is insensitive to the choice of initial conditions.

A time interval of $T_F = 5$ days is used in the results shown, but using longer periods does not alter the long-term results, only the time taken to converge (see Fig. S3). For each time period T_F, the size-spectrum model is solved using the method of lines. This involves using finite difference approximations for the x derivatives (using a mesh spacing $\delta x = 0.1$) in Eq. (1) to obtain a system of coupled ordinary differential equations (Shiesser, 1991), which are solved using the Matlab solver *ode15s*. At the end of the time period, individual catches Y_i are calculated using Eq. (6) and each fisher has a probability q_i of changing to a new target size. Once the new target sizes are chosen, the aggregate fishing mortality for the next time period is calculated using Eqs. (4) and (5). This process is repeated for a total time period of 10 years and the final size spectrum, productivity, aggregate fishing mortality rate and aggregate yield are calculated. Productivity $p(x,t)$ is defined as the product of biomass density $w_0 e^x u(x,t)$ and mass-specific somatic growth rate $\varepsilon(x,t)g(x,t)$. This is the total rate of biomass production in fish of log body mass x and has dimensions mass per unit volume of water per unit time (Garcia et al., 2012; Law et al., 2015b). Reproductive output is redirected into individuals of egg size w_0 and so this is not counted in the productivity at body mass $w_0 e^x$. After 10 years, all simulations shown had settled into a statistically stationary state in which the individual fishers' target masses $x_{f,i}$ are still changing stochastically, but the aggregate fishing mortality, yield and stock biomass are no longer changing substantially.

The overall fishing pressure is the product of the number of fishers N_F and the individual fishing mortality parameter F_0. We investigate the consequences of increasing fishing pressure in a controlled way by increasing the parameter N_F while holding $F_0 = 0.01\ \mathrm{yr}^{-1}$ constant. However, the results are similar if F_0 is increased with N_F held constant.

Results

Theoretical predictions

When a fixed number of fishers adjust their net mesh sizes to increase their individual biomass catch in the absence of size-based regulations, and undistorted by market prices, the predicted steady state is a Nash equilibrium (Nash, 1951). This means that each fisher obtains the same return (i.e. same biomass catch) and any change in behaviour of an individual fisher leads either to no change or to a reduction in that individual's return. In the range of sizes being targeted, the biomass density must be a constant b^* because, if the biomass density were greater than b^* in any size range, a fisher could increase his/her catch by switching to a net size in that range. This constant biomass spectrum is predicted to emerge as a result of the two-way interaction between the aggregate fishing mortality and the dynamics of the fish stock. However, the fishers make decisions simply by comparing their own catch to that of others and are not assumed to have any knowledge of the ecological dynamics. Importantly, these predictions are not limited to a specific ecological model for the dynamics of the fish stock.

Simulation results

Figure 1 shows the results of simulating the coupled fishing-size-spectrum model for African catfish. When the number of fishers is small, fishing has virtually no impact on the biomass spectrum (Fig. 1a). Although fishers sample the full range of body sizes, their adaptive behaviour takes most of them close to a unique target size, around 300 g, at which biomass is greatest (Fig. 1b). This convergence in target sizes is the emergent outcome of the agent-based fishing model that results from fishers randomly exploring different target sizes until they hit on a target size that gives a high yield, making them less likely to switch.

As the number of fishers increases, the biomass of fish of around 300 g is depleted and this makes it more likely for fishers to abandon this target size and explore other target sizes. Fishers now exploit a broader range of body sizes (1 g to 300 g), with more fishing on smaller fish to the left of the biomass peak where the productivity is higher (Fig. 1d).

This results in a change in the shape of biomass density from its unfished state to a state where it is flat-topped in the range 1 g to 300 g (Fig. 1c). A further increase in the number of fishers widens the range over which the biomass spectrum is flattened (Fig. 1e,g), with a smaller cluster of fishers remaining at the location of the original biomass peak (Fig. 1f,h). This outcome is close to the Nash equilibrium because the biomass spectrum is close to constant in the exploited size range and there is little variation in catch among individuals: 99% of fishers in Fig. 1h obtain a catch that is within 5% of the maximum individual catch. The location of the productivity peak shifts as more fishers join the fishery, but fishers almost always target body sizes above the productivity peak because they obtain greater catches by doing so. **In Fig. 1h, the aggregate fishing mortality is approximately proportional to the size-dependent productivity of the stock over the exploited size range. This corresponds to BH of a single species** and is consistent with the ideal free distribution, where predation effort is proportional to the rate at which prey biomass is produced (Kacelnik et al., 1992).

Figure 2 shows how, as the number of fishers increases without size regulations, the range of sizes being targeted expands downwards to include smaller fish and the mean size of fish in the catch decreases. These are conventionally interpreted as signs of overfishing (Welcomme, 1999; Tweddle et al., 2015). However, it is important to note that, although small fish comprise an increasing proportion of the catch at higher fishing pressure, large fish are not completely fished out (Fig. 1e). Instead, as large fish start to become depleted, it becomes more attractive to target smaller fish than to drive the abundance of large fish down further.

Figure 3 shows simulation results when the fishers are prohibited from targeting body masses below 100 g. The outcome at low fishing pressure is similar to the case without size regulations: the fishers can still target the biomass peak at a body mass of around 300 g (Fig. 3a,b). However, as the number of fishers increases, they are prevented from expanding the target size range down below 100 g; instead, the majority of fishers target fish of the minimum allowed size (Fig. 3c,d). This results in greater depletion of large fish than in the case without size regulations (compare the truncation of the biomass spectrum at the right-hand end of the graph in Fig. 3c with Fig. 1c).

Figure 4 shows the aggregate yield as the number of fishers increases without size regulations, and with minimum allowed target sizes of 10 g, 100 g and 250 g. All four cases have a maximum sustainable yield (MSY) at intermediate fishing pressure. The case without size regulations gives the highest MSY and imposing minimum size regulations of 10 g, 100 g and 250 g systematically reduces MSY. With any size-selectivity pattern, overfishing can occur if the number of fishers is above the point corresponding to MSY. **In addition, sudden stock collapse can occur if the fishing pressure is too high, so it would be advisable to ensure the fishing pressure is significantly below that corresponding to MSY (for example, the example with 6,000 fishers shown in Fig. 1g,h is a very dangerous level for the fishery to operate).** Without size regulations, the stock can support around 5000 fishers at MSY; this number reduces to 3000 with a minimum target size of 10 g and to 1200 with a minimum target size of 100 g or 250 g. Without size regulations, stock collapse at around 7000 fishers; with minimum target sizes of 10 g and 100 g, stock collapse occurs at around 4500 and 2000 fishers respectively. It is possible to protect the stock from collapse by imposing a sufficiently large minimum target size of 250 g, as this ensures that a sufficient number of fish always reach maturity. However, it is clear that doing this sacrifices a large potential yield and is not in itself sufficient to prevent overfishing.

To check how robust our results are to model selection, we tested the following alternative scenarios for fisher behaviour, which are described in more detail in Supporting Information, section 2. Model 2: fishers have some knowledge of the size structure of the stock and a more likely to choose a target size where the biomass density is high. Model 3: fishers make large, random changes to their target size when their catch is low, but small, incremental adjustments when their catch is high. Model 4: fishers have some knowledge of their competitors' target sizes and catches and copy the behaviour of a successful competitor. Results are shown in Fig. S3. In addition, we ran the simulations with the size-spectrum model parameterised for a different species, Atlantic mackerel (*Scomber scombrus*) (Fig. S4), with a longer time period of $T_F = 60$ days between opportunities for the fishers to change target size (Fig. S5) and with the inclusion of random variation in the fishing mortality and size selectivity of individual fishers (Eq. S9 and Fig. S6). **We also tested the effects of random yearly variations in reproduction (Fig. S7) and of replacing the fixed resource spectrum with a von Bertalanffy growth function (Fig. S8).** All of these alternative models show the emergence of a flattened biomass spectrum and a close match between fishing mortality and productivity.

Discussion

Balanced harvesting (BH) has been proposed as a basis for the ecosystem approach to fishing (Misund et al., 2002; Zhou et al., 2010; Garcia et al., 2012, 2015c) and is rightly coming under increasing scrutiny (Froese et al., 2015; Froese et al., 2016b). Among the criticisms of BH are that it would require an impractical and level of micro-management (Andersen et al., 2015; Reid et al., 2015) and that the costs of implementation would exceed any economic benefit (Burgess et al., 2015; Charles et al., 2015). At a single-species level, balanced harvesting requires adjusting the level of fishing mortality according to the productivity of fish of different sizes (Garcia et al., 2012). Implementing of this fishing pattern may appear *prima facie* to be very difficult, requiring size-based quotas, productivity data and catch monitoring (Garcia et al., 2015b). However, our results provide a counter to this argument by showing that BH of a single species can, in some circumstances, emerge as a result of individual fishers' attempts to maximise their biomass catch, without externally imposed size-based regulations or monitoring.

This result has its origin in a simple, conceptual framework for individual fishers' size selectivity: Nash equilibrium requires that all fishers obtain the same biomass catch and the ideal free distribution implies that fishing effort is distributed in proportion to productivity. We tested the emergence of the Nash equilibrium and ideal free distribution in a single-species size spectrum model coupled with a simple toy model for fishers' choice of gillnet mesh size. These models do not accurately replicate the dynamics of a multi-species ecosystem, nor the complexity of real human behaviour. However, they do show that a balanced fishing pattern can emerge without either size-based regulations or the need for cooperative behaviour among fishers. This result comes with a number of caveats which we now discuss.

The match between fishing mortality and productivity is an equilibrium result and we do not claim that it applies when the system is away from equilibrium. In fact, as our results at low fishing pressure show, fishing mortality is initially concentrated on sizes where the biomass, and therefore the catch per unit effort, is highest. Increasing fishing pressure reduces the biomass at these sizes over time, resulting in a flattening of the biomass spectrum. There is a complex interplay between fishing mortality, biomass and productivity at different sizes as this unfolds and the exact nature of these time-dependent dynamics warrants further investigation.

Our model assumes that fish of all sizes are have equal value per unit mass and that individual fishers' objective is to maximise the biomass of their catch. In commercial fisheries, large fish typically attract a much higher unit price than do small fish (Sethi et al., 2010; Tsikliras and Polymeros, 2014). However, for small-scale fisheries in areas where there is poverty and malnutrition, the provision of biomass for food is more important than the market value of the catch (Beveridge et al., 2013; FAO, 2014). Small fish are often preferred in these communities as they are easily sundried and require minimal fuel for cooking (Kawarazuka and Béné, 2011; Longley et al., 2014; Kolding et al., 2016b). Our framework can also be extended to include a dependence of market price p per unit mass (or catchability q) on body size x. In this situation, the return to a fisher targeting body size x is $p(x)q(x)b(x)$, where $b(x)$ is the standing biomass density. The Nash equilibrium still requires that each fisher obtains the same return, so pqb must be constant within the exploited size range. This means that the biomass spectrum would be depleted more at body sizes whether either the catchability or the unit price is relatively high **(or where the unit cost of targeting fish is relatively low).** This is consistent with observations in commercial fisheries of steepening of the size spectrum caused by heavy depletion of high-value, large fish (Rice and Gislason, 1996; Blanchard et al., 2005; Hsieh et al., 2010; Shephard et al., 2012; Tsikliras and Polymeros, 2014). The Nash equilibrium predicts that, at low fishing pressure, fishers will target the body size where pqb is maximal and, as fishing pressure increases, will flatten pqb over an expanding range of exploited sizes. The precise details of the emergent fishing pattern that produces this outcome as fishing pressure increases will be the subject of future work.

BH by itself is not a safeguard against overfishing: controls on fishing pressure, for example via total allowable catch, are needed whether or not the pattern of size-selectivity is balanced (Law et al., 2015a). But our results suggest that minimum-size restrictions without effort control will either increase fishing pressure on large individuals, or reduce the number of fishers that the fishery can support. This finding is consistent with results from Lake Kariba showing that, without size restrictions, fishers target progressively smaller sizes as fishing pressure increases, but that this results in higher yields than selectively targeting larger fish (Kolding et al., 2016a).

We do not claim that the Nash equilibrium gives the maximum sustainable aggregate yield; including more sophisticated types of behaviour could generate greater yields, for example by including cooperation among fishers (Sumaila, 1999; Mashanova and Law, 2005). Our finding is just that the biomass yield is greater than that obtained by restricting fishing to a relatively unproductive part of the size spectrum. The model applies in the case where the impact of a single agent on the fish stock is small. This is a reasonable model of individual fishers in a small-scale fishery, but would not apply if, for example, each agent represented a commercial fishing organisation capable of having a major effect on the stock.

We have studied a model for a single fish species with the aim of understanding how individual-level decisions scale up to emergent patterns of aggregate fishing mortality. In reality, productivity is dependent on species as well as body size and it is an open question how emergent fishing mortality would be distributed in a multi-species community. We have used the simplest possible model for fishers' choice of target body size for two main reasons: (i) we are interested in emergent phenomena and these results are at their most powerful when the simplest possible assumptions are made about individual behaviour (Axelrod, 1997); (ii) fishers in small-scale fisheries are often operating with limited information and only have their daily catch rates as guidance to which catch method they choose. We do not claim that all types of individual decision-making will result in BH and the limitations on fisher behaviour that allow BH to emerge need to be investigated further.

Different models of the ecological dynamics produce quite different predictions for productivity (Christensen et al., 2005; Froese et al., 2008; Jacobsen et al., 2014; Law et al., 2015b; Andersen et al., 2016) and this is a matter of ongoing research. At equilibrium, productivity is known to be proportional to cohort biomass (Law et al., 2015b) and YPR models typically predict that the peak in cohort biomass is close to the size at maturity (Beverton and Holt, 1957; Froese, 2004). This issue does not affect our main conclusion, which is that fishing effort will become distributed in proportion to productivity, regardless of whether small fish are more productive than large ones or vice versa. However, it is important to recognise that increasing levels of fishing pressure will change the relative productivities of different body sizes (as seen for example in Fig. 1).

Figure 5 shows the yield spectra of a small-scale, artisanal fishery in the Bangweulu Swamps of Northern Zambia, which is largely non-compliant with size-based regulations, and a highly-regulated commercial fishery in the Celtic Sea, which operates *inter alia* with mesh-size restrictions and minimum landing sizes (see Supporting Information, section 3). In the Bangweulu Swamps, fish as small as 10 g and as large as 10 kg form a substantial part of the catch, and this has been stable over the last 50 years (Kolding et al., 2003). This shows that a small-scale fishery operating without size-based regulations can sustainably catch small fish while preserving larger fish in the ecosystem. This is consistent with the predictions of our agent-based fishing model, although not directly comparable with model results, which are for a single fish species (and not therefore intended as model validation).

In contrast, in the Celtic Sea, fish less than about 250 g do not form a major part of the landed catch. During the period of data collection, smaller fish were also caught, but were discarded before landing. The absence of small fish from the catch is likely due to a combination of factors, including mesh size regulations, minimum landing sizes, quotas and economic drivers. Moreover, the results do not imply that commercial fisheries such as the Celtic Sea could sustainably expand to smaller fish at present. These fisheries typically have high fishing mortality on big fish. It would be dangerous to increase fishing mortality on small fish without first reducing fishing mortality on low-productivity fish and allowing the structure of the fish community to readjust. Nonetheless, the data show that there is a potential catch of relatively small fish that is currently being discarded and could be retained if the main priority were the maximisation of catch biomass for food.

Applying the concept of a Nash equilibrium to a fishery where individual fishers must choose what size fish to target is a powerful approach because it make predictions that are not limited to a specific model for resource dynamics, a particular species, or particular set of gears. The requirement that all agents obtain the same return at Nash equilibrium implies that the biomass density of fish must be the same at all exploited sizes (Sheldon et al., 1972; Boudreau and Dickie, 1992), or conversely that the fishers exploit those sizes at which the biomass of fish is maximal. Real fisheries will deviate from the fishing patterns and catch distributions shown in Fig. 1 because of the imperfect size-selectivity of the gears that are available in practice, **and because of limits on the ability of fishers to change their size selection**. Nonetheless, our model predicts a widespread organising principle in which fishing effort tends to becomes distributed over body size in such a way as to equalize returns from targeting different sizes.

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Table 1. Parameter values for the size-spectrum model representing African catfish. Length at first maturity is approximately 30.8 cm (Fishbase, www.fishbase.org/summary/1934) and asymptotic length 67.5 cm (Kolding et al., 2003). Length l is converted to mass w using $w = al^b$ with $a = 0.008\ \mathrm{g\ cm}^{-b}$ and $b = 2.983$ (Kolding et al., 2003). Other parameter values are the same as in Law et al. (2015b).

Parameter		**Value**
w_0	Egg mass	0.001 g
w_m	Mass at 50% maturity	220 g
w_∞	Asymptotic mass	2290 g
ρ_m	Controls the body mass range over which maturation occurs	10
ρ	Exponent for approach to asymptotic body mass in reproduction function	0.2
ε_0	Proportion of reproductive output that is converted into egg production	0.5
K	Food conversion efficiency	0.2
α	Search rate scaling exponent	0.8
A	Feeding rate constant	750 $\mathrm{m}^3\ \mathrm{g}^{-\alpha}\ \mathrm{yr}^{-1}$
β	Mean log predator:prey mass ratio	5
σ	Diet breadth	2.5
μ_0	Intrinsic (non-predation) mortality rate at birth	0.2 yr^{-1}
ξ	Exponent for intrinsic (non-predation) mortality	0.15
$x_{0,\max}$	Greatest body mass of plankton	0.02 g
u_0	Plankton density at body mass 1 mg	200 m^{-3}
γ	Exponent of plankton spectrum	2

Figure legends

Figure 1. Simulated fishers without size regulations self-organise to produce a flat biomass spectrum and an aggregate fishing mortality that is proportional to productivity. (a,c,e,g) Biomass spectrum of the unexploited (dashed) and exploited (solid) systems. **(b,d,f,h)** Productivity (dashed) and aggregate fishing mortality (solid) as a function of body mass. **(a,b)** 75 fishers. **(c,d)** 1200 fishers. **(e,f)** 3000 fishers. **(g,h)** 6000 fishers. Results are shown after running the model for a total period 5 years with updating of fishing gear at time intervals of $T_F = 5$ days.

Figure 2. Increasing the number of simulated fishers without size-based restrictions results in smaller fish being caught. Number of fishers against: the mean size of fish in the catch (dashed); the body size range over which the biomass spectrum is approximately flat (the two solid curves show the body sizes between which biomass density is within 10% of its maximum value), which approximately corresponds to the body size range being targeted by the fishers. Results are shown after running the model for a total period 5 years with updating of fishing gear at time intervals of $T_F = 5$ days. Dotted vertical lines correspond to the three fishing intensities shown in Fig. 1.

Figure 3. Simulated fishers operating under a minimum size regulation target fish close to the minimum allowed size. (a,c) Biomass spectrum of the unexploited (dashed) and exploited (solid) systems. **(b,d)** Productivity (dashed) and aggregate fishing mortality (solid) as a function of body mass. **(a,b)** 75 fishers. **(c,d)** 1200 fishers. Results are shown after

running the model for a total period 5 years with updating of fishing gear at time intervals of $T_F = 5$ days and with a minimum allowed target size of 100 g.

Figure 4. Imposing minimum size regulations on the simulated fishers reduces aggregate yield and can cause stock collapse at lower fishing pressure. Number of fishers against: sustainable aggregate biomass yield without size-based restrictions (solid) and with a minimum target size of 10 g (dash-dot), 100 g (dashed) and 250 g (dotted). Results are shown after running the model for a total period 5 years with updating of fishing gear at time intervals of $T_F = 5$ days. Dotted vertical lines correspond to the three fishing intensities shown in Fig. 1.

Figure 5. Empirical yield spectra from the Bangweulu Swamps and the Celtic Sea. Yield spectra calculated from catch data disaggregated by body mass from: a small-scale fishery without size-based regulations in the Bangweulu Swamps (blue); a highly regulated commercial fishery in the Celtic Sea (landings, green and landings+discards, red).

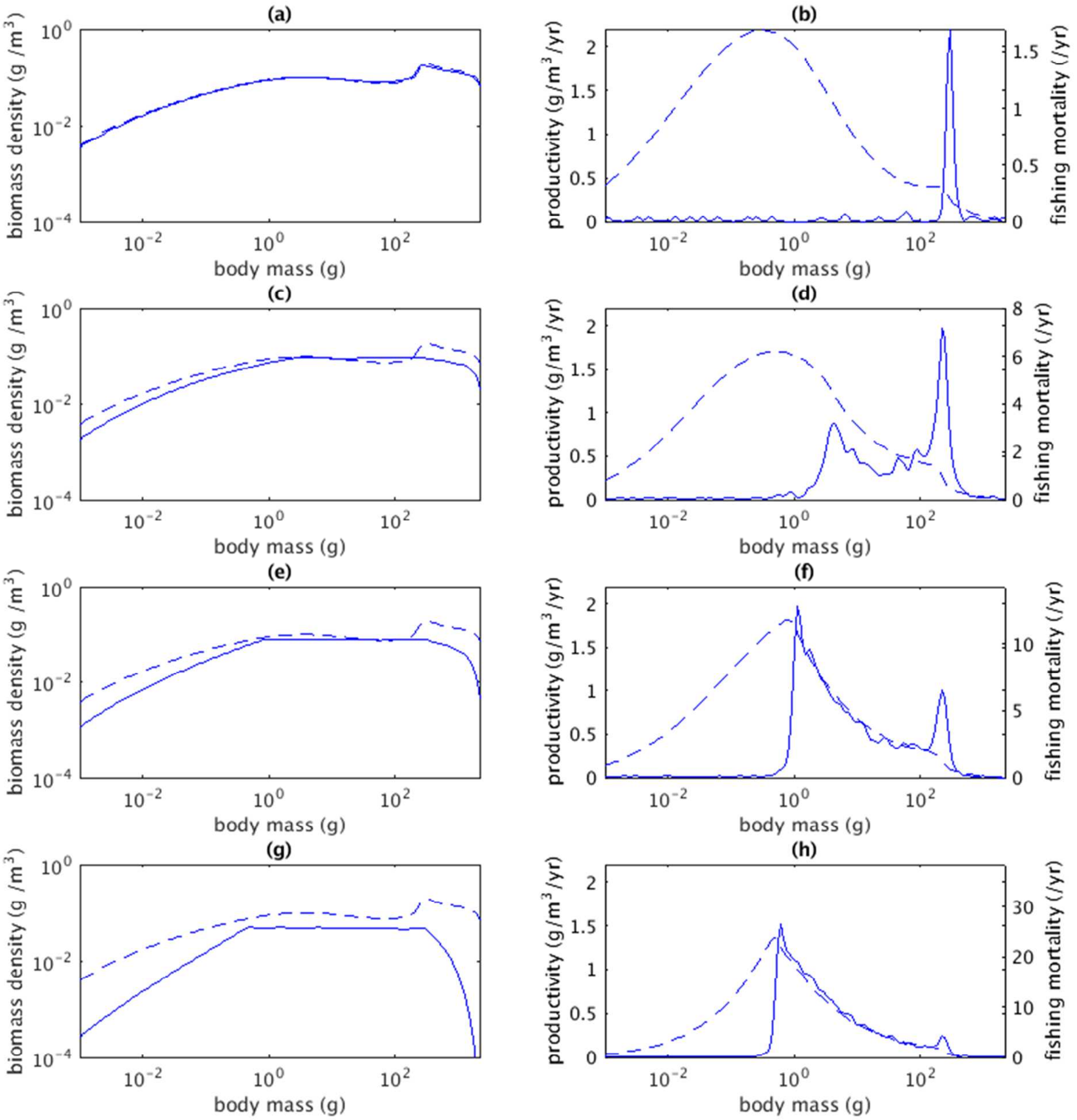

(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
biomass density (g /m^3)
productivity (g/m^3/yr)
fishing mortality (/yr)
body mass (g)
10^{0}
10^{-2}
10^{-4}
10^{2}
0
0.5
1
1.5
2
2
4
6
8
5
10
20
30

Figure 1

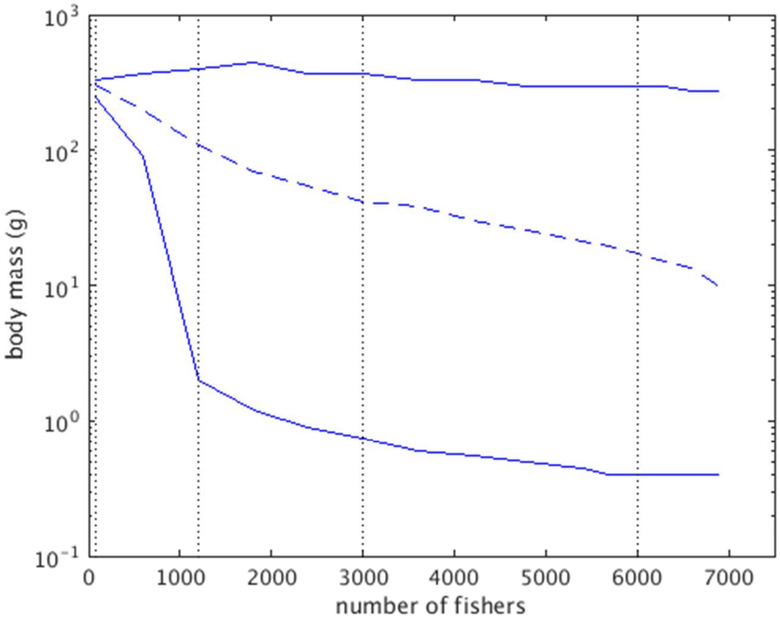
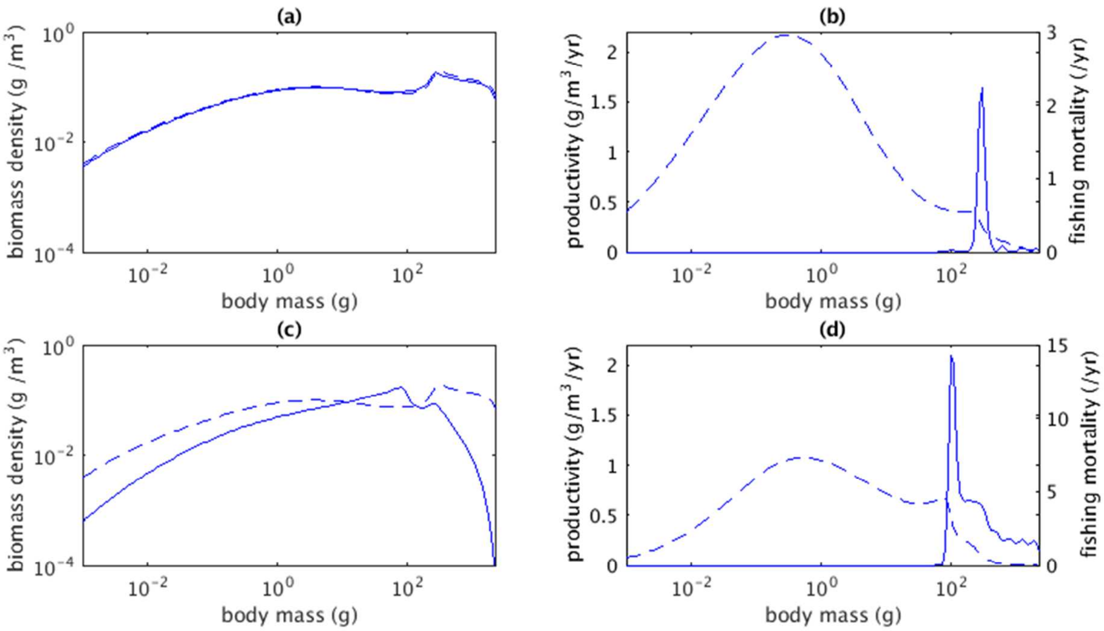
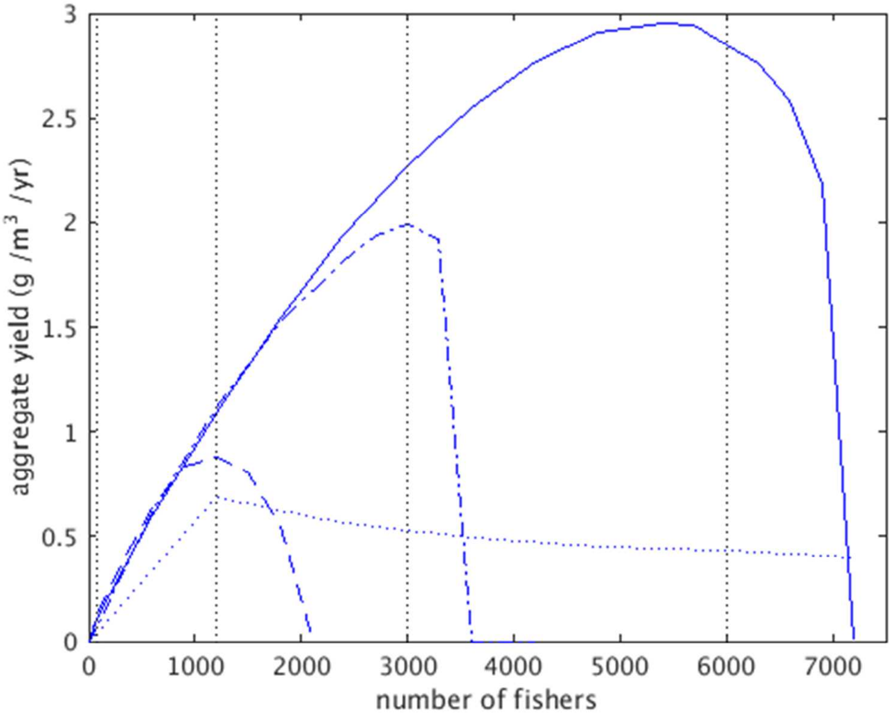

body mass (g)
10^3
10^2
10^1
10^0
10^{-1}
0
1000
2000
3000
4000
5000
6000
7000
number of fishers

Figure 2



694

695 Figure 3



696

697 Figure 4

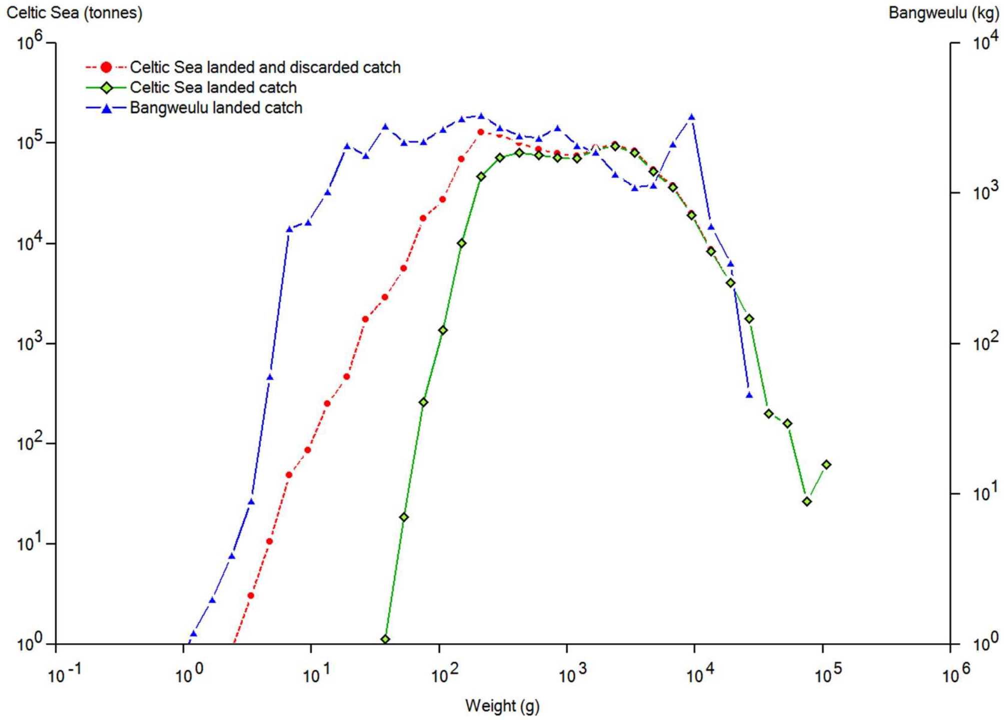

Celtic Sea (tonnes)
Bangweulu (kg)
Celtic Sea landed and discarded catch
Celtic Sea landed catch
Bangweulu landed catch
10^6
10^5
10^4
10^3
10^2
10^1
10^0
10^4
10^3
10^2
10^1
10^0
10^{-1}
10^0
10^1
10^2
10^3
10^4
10^5
10^6
Weight (g)

Figure 5

Balanced harvesting can emerge from fishing decisions by individual fishers

Supporting Information

1. Dynamic size-spectrum model

Here we provide the complete equation set for the size-spectrum model. A full derivation of the model can be found in Law et al. (2015).

McKendrick–von Foerster equation for size-structured dynamics	$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial x}(\varepsilon g u) - (\mu + F)u + R\delta(x)$	(S1)
Mass-specific food intake rate	$g(x,t) = AKe^{(\alpha-1)x} \int e^{x'} s(e^{x-x'}) \left(u(x',t) + u_r(x')\right)dx'$	(S2)
Natural mortality rate	$\mu(x,t) = A \int e^{\alpha x'} s\left(e^{x'-x}\right) u(x',t)dx' + \mu_o(x,t)$	(S3)
Feeding kernel	$s(e^r) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(r-\beta)^2}{2\sigma^2}\right)$	(S4)
Fixed resource spectrum	$u_r(x) = \begin{cases} u_0 e^{-(1-\gamma)x} & x \leq x_{0,\max} \\ 0 & \text{otherwise} \end{cases}$	(S5)
Non-predation mortality rate	$\mu_o(x,t) = \mu_0 e^{-\xi x} \frac{g(0,t)}{g(x,t)}$	(S6)
Proportion of assimilated prey biomass used for somatic growth	$\varepsilon(x) = 1 - \frac{e^{\rho(x-x_\infty)}}{1 + e^{-\rho_m(x-x_m)}}$	(S7)
Population reproduction rate	$R(t) = \varepsilon_0 \int_0^{x_\infty} \left(1 - \varepsilon(x)\right) g(x,t)u(x,t)e^x dx$	(S8)

To ensure that the size-spectrum model produces realistic growth trajectories, we adjusted the model parameter u_0 describing the abundance of the fixed plankton resource (see Table 1) so that the size-at-age curve predicted by the size-spectrum model provides a good match with the von Bertalanffy growth model for African catfish (Kolding et al., 2003). This required a higher value for u_0 than that estimated in previous studies (Law et al., 2015), but this parameter is expected to vary with the primary productivity of the ecosystem and the simulation results are not sensitive to the value of u_0. Figure S1 shows the size-at-age curves predicted by the size-spectrum model (in unexploited and exploited states), together with the von Bertalanffy model. The discrepancy between the two curves at early ages is because the von Bertalanffy model does not accurately capture the growth of juveniles (the von Bertalanffy weight at age 0 is 26.8 g), whereas individuals in the size-spectrum model have body mass 0.001 g at age 0 representing the mass of an egg.

The size-spectrum model assumes that all the reproductive output from mature females is converted in viable eggs of mass 0.001 g. Therefore, the relationship between spawning stock biomass (SSB) and model egg production is linear and not density-dependent. However, survival of eggs to a given age or size depends on: (i) how quickly they can grow, which depends on the abundance of prey; and (ii) how likely they are to be predated, which depends on the abundance of predators. Therefore, if recruitment is taken to mean survival to a given age or size, then there is a density-dependent relationship between SSB and recruitment. Equilibrium model recruitment can be calculated as the product of total reproductive output R in Eq. (S8) and the probability P_{recruit} of survival to size x_{recruit} (Law et al., 2015):

$$P_{\mathrm{recruit}} = \exp\left(-\int_0^{x_{\mathrm{recruit}}} \frac{\mu(x)}{g(x)\varepsilon(x)}\,dx\right)$$

Hence, rather than being an externally specified assumption, the relationship between SSB and recruitment is a model output. Figure S2 shows a graph of SSB (calculated as the total biomass of fish larger than the maturity midpoint x_m) against recruitment to size 1 g. The right-hand end of this curve corresponds to the unexploited state. Increasing the number of fishers decreases SSB and therefore egg production. Initially, reduction of SSB has little effect on recruitment (recruitment curve is relatively flat down to about SSB = 0.05 g/m^3). This is because decreased egg production is counterbalanced by increased survival probability due to reduced predation. Below around SSB = 0.05 g/m^3, recruitment starts to fall off rapidly towards zero as the population collapses.

2. Alternative models and supplementary simulation results

We simulated four different stochastic models for individual fishers' choice of target fish size. Each model has two main ingredients: the probability of changing target size and the rule for how the new target size is chosen. These are summarized in Table S1. Model 1 is the model described in the main text. Model 2 assumes that the fishers have knowledge of the size structure of the stock and, when they change gear, are more likely to choose a target size where the current biomass density (and hence the current catch per unit effort) is high. This is implemented by defining a probability density function $P(x_{f,i})$ for the choice of new target size $x_{f,i}$ that is proportional to the current biomass spectrum. In model 3, fishers make random, normally distributed adjustments to their target size. The variance of the normal distribution is high when the individual fisher's catch (relative to the maximum catch) is low and vice versa. Hence, fishers are likely to quickly move away from target sizes that produce small catches and to stick around parts of the size spectrum that produce high catches. This is a type of kinetic mechanism for random relocation (Codling et al., 2008). Model 4 assumes that fishers have some knowledge of the behavior and catches of their competitors. At each time interval, each fisher chooses a competitor and switches to that fisher's current target size (with a small amount of random noise to avoid the whole population collapsing onto exactly the same target size). The competitor to copy is chosen with a probability that is proportional to that competitor's current catch, i.e. fishers are more likely to copy a competitor with a high catch than to copy one with a low catch.

Figure S3 shows simulation results for the alternative models. Although the amount of noise in the results and the time taken to converge very with the different models, all four cases show the emergence of a flattened biomass spectrum and a correspondence between the aggregate fishing mortality and the productivity.

Figure S4 shows a similar set of simulation results as Fig. 1 in the main text, but with the size-spectrum model parameterized for a different species, Atlantic mackerel. The estimated parameters for Atlantic mackerel are asymptotic mass of $w_\infty = 650$ g, maturation midpoint of $w_m = 200$ g, mean log predator:prey mass ratio of $\beta = 6$ and plankton density parameter of $u_0 = 100$ m^{-3} (Law et al., 2015). Figure S5 shows the same simulations as Fig. 1 but with a longer period of $T_F = 60$ days between opportunities for the individual fishers to change their target size.

We also tested the effect of introducing random noise into the fishing mortalities and size selectivities of individual fishers. To implement this, Eq. (4) for the i^{th} agent's fishing mortality $F_i(x)$ is replaced by

$$F_i(x) = \frac{F_{0,i}}{\sigma_{F,i}\sqrt{2\pi}} \exp\left(-\frac{\left(x - x_{f,i}\right)^2}{2\sigma_{F,i}^2}\right), \tag{S9}$$

At each time interval, the $F_{0,i}$ are set to be independent, identically distributed (IID) normal random variables with mean F_0 and standard deviation $0.2F_0$; the $\sigma_{F,i}$ are set to be IID normal random variables with mean σ_F and standard deviation $0.2\sigma_F$ $(i = 1, \dots N_F)$. To allow for the fact that variations in individual fishers' catches can now be due to noise in $F_{0,i}$ as well as variations in the biomass of fish of the target size, we use the ratio of catch to fishing intensity $C_i = Y_i/F_{0,i}$ as the variable determining the probability of changing target size, so the probability of the i^{th} fisher changing target size is $q_i = 1 - C_i/C_{\max}$. The simulation results are shown in Fig. S6.

To test the effects of yearly fluctuations in recruitment, we ran simulations where the egg production parameter ε_0 was not constant but set to a different value each year. We used a log-normal distribution so that $\ln(\varepsilon_0)$ is normally distributed with mean $\ln(0.5)$ and standard deviation 0.5. Results are shown in Fig. S7. Relative to the results with fixed $\varepsilon_0 = 0.5$, there is more noise in the distribution of fishing mortality at any given point in time. There is also more variability over time, with higher biomass and productivity following years of strong reproduction. As the total number of fishers in this simulation is fixed, the level of fishing pressure relative to productivity is lower following years of strong reproduction. In these years (e.g. at $t = 2$ yr in Fig. S7), the peak in fishing mortality at a body mass of around 300 g is more pronounced. This higher fishing mortality is required to bring the peak in the unexploited biomass down to the level of the rest of the biomass spectrum, as seen in the standard model with fixed ε_0 (see Fig. 1). Following years of weaker reproduction (e.g. at $t = 1$ yr in Fig. S7), the fishing pressure is higher relative to productivity and the fishing pattern more closely resembles that seen at high fishing pressure in the standard model.

Finally, we tested some of the assumptions of the size-spectrum model by replacing the fixed resource spectrum $u_r(x)$ with an externally specified von Bertalanffy growth function. Specifically, Eq. (S2) was replaced by

$$g(x,t) = AKe^{(\alpha-1)x}\int e^{x'}s\left(e^{x-x'}\right)u(x',t)dx' + 0.5g_{VB}(x)$$

where

$$g_{VB}(x) = bk\left(\exp\left(\frac{x_\infty - x}{b}\right) - 1\right)$$

This is the mass-specific growth rate (i.e. $1/w\ dw/dt$) at log body mass $x = \ln(w/w_0)$ under a von Bertalannfy growth model with growth parameter k and length-weight exponent b. To reduce the contribution of cannibalism to growth and mortality, we reduced the predation parameter A by a factor of 2 and increased the intrinsic, density-independent mortality parameter μ_0 by a factor of 2. Overall, these changes move the model away from a situation where growth and mortality above a certain size are dominated by cannibalism to a mixture of cannibalism and externally specified, density-independent growth and mortality rates. The results of applying agent-based fishing to this model are shown in Fig. S8 and still display the emergence of a flattened biomass spectrum and a close match between aggregate fishing mortality and productivity.

3. Empirical catch data

The fishery in the Bangweulu Swamps is largely non-compliant with external regulations (Kolding et al., 2003) and closer to being self-organised (in the sense of this paper) than any other fishery for which size-based catch data are available. The fishery has been relatively stable for at least the last 50 years (the period over which data exist), with about 5,000 fishers catching approximately 15,000 ton yr^{-1} (see Table 2 of Kolding et al., 2003). The fishery is isolated and is the most important source of protein for the local population, as animal husbandry is constrained by tsetse flies. Catch data for the Bangweulu Swamps are a representative sample of the multispecies yield spectra, obtained from monitoring the daily total catch of 16 fishers for 2 years (1994-1996), aggregating by species and disaggregating by length (Kolding et al., 2003; Ticheler et al., 1998). Length l was converted to weight w using $w = al^b$ with species-specific values of a and b given in Table 8 of Kolding et al. (2003).

The Celtic-Sea demersal fishery operates with mesh-size restrictions and minimum landing sizes. It mostly uses trawl gears, with catches of around 100,000 to 150,000 ton yr^{-1} from over 1,000 active vessels. Landed and discarded weights of demersal fish species in the Celtic Sea area were obtained from the Scientific, Technical and Economic Committee for Fisheries (http://datacollection.jrc.ec.europa.eu/dd/effort accessed on 29/05/2015). Data from ICES divisions VIIb-k during the period 2003-13 were used. Spanish data for the years 2003-2011 were not available; the missing data were estimated from the proportion of Spanish catches for 2012-13 for each species under the assumption that the relative contribution of the Spanish catches remained stable over time. This resulted in an overall increase of 8% for the years with missing data. The fourteen demersal fish species (or species groups) that contributed > 95% of the international catches were selected: *Merluccius merluccius, Lophius spp, Melanogrammus aeglefinus, Lepidorhombus spp, Merlangius merlangus, Gadus morhua, Rajidae, Pleuronectes platessa, Pollachius virens, Microstomus kitt, Molva molva, Glyptocephalus cynoglossus, Solea solea* and *Pollachius pollachius*. The remaining species (< 5% of the catch) were excluded because of a lack of reliable length data. Length-frequency distributions and length-weight relationships of the landings and discards for these 14 species were obtained from sampling by the Marine Institute (Ireland). These data were assumed to be representative of the international catches. The length data were converted to biomass of the total catch and binned in logarithmically spaced intervals.

Supporting information references

1. Codling EA, Plank MJ, Benhamou S (2008) Random walk models in biology. Journal of the Royal Society Interface, 5:813-834.
2. Kolding J, Ticheler H, Chanda B (2003) The Bangweulu Swamps – a balanced small-scale multi-species fishery. In Jul-Larsen E, Kolding J, Nielsen JR, Overa R and van Zwieten PAM (eds.) Management, co-management or no management? Major dilemmas in southern African freshwater fisheries. Part 2: Case studies, pp. 34-66 FAO Fisheries Technical Paper 426/2. FAO, Rome.
3. Law R, Plank MJ, Kolding J (2015) Balanced exploitation and coexistence of interacting, size-structured, fish species. Fish and Fisheries, early access online doi: 10.1111/faf.12098.

4. Ticheler HJ, Kolding J, Chanda B (1998). Participation of local fishermen in fisheries data collection: a case study from the Bangweulu Swamps, Zambia. Fisheries Management and Ecology, 5:81–92.

Table S1. Definition of alternative agent-based models for fishers' choice of target size. Each model is specified by two ingredients: (i) the probability q_i of each agent changing their target size at each time interval T_F; (ii) the algorithm for setting the new target size $x_{f,i}$. $\mathrm{Uni}[0, x_\infty]$ is a uniform random variable between 0 and x_∞; $N(0,1)$ is a standard normal random variable.

Model	Description	Probability q_i of changing target size	New target size $x_{f,i}$
1	Probability of changing target size increases as catch decreases; new target size chosen completely randomly.	$1 - Y_i/Y_{\max}$	$\mathrm{Uni}[0, x_\infty]$
2	Probability of changing target size increases as catch decreases; new target size is more likely to be chosen where biomass density is high.	$1 - Y_i/Y_{\max}$	Probability density function: $P(x_{f,i}) = b(x_{f,i}) / \int_0^{x_\infty} b(x)dx$
3	Change in target size is small when catch is high and large when catch is low.	1	$x_{f,i} + (1 - Y_i/Y_{\max})x_\infty/4\ N(0,1)$
4	Copy a successful competitor's target size	1	$x_{f,K} + 0.5N(0,1)$, where $\Pr(K = k) \propto Y_k$

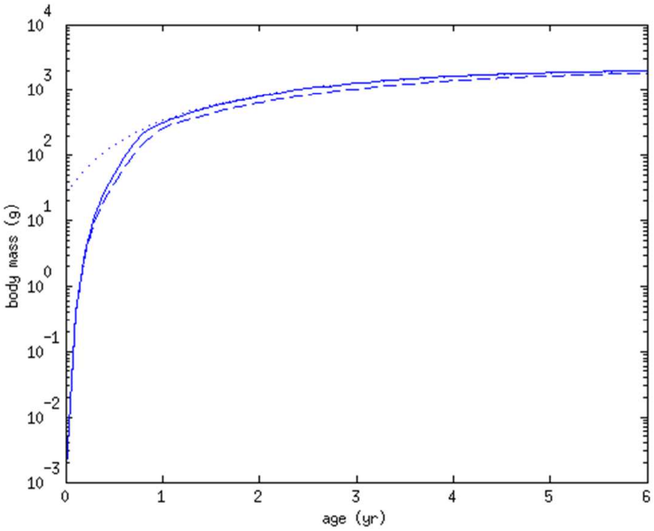


Figure S1. Size-at-age curve for African catfish predicted by the size-spectrum model in the unexploited state (solid), exploited state with 3000 fishers (dashed) and estimated von Bertallanfy growth curve $w = w_\infty\left(1 - e^{-k(t-t_0)}\right)^b$ (dotted) with $k = 0.51$ yr^{-1}, $w_\infty = 2290$ g, $b = 2.983$, $t_0 = -0.5$ yr (Kolding et al., 2003).

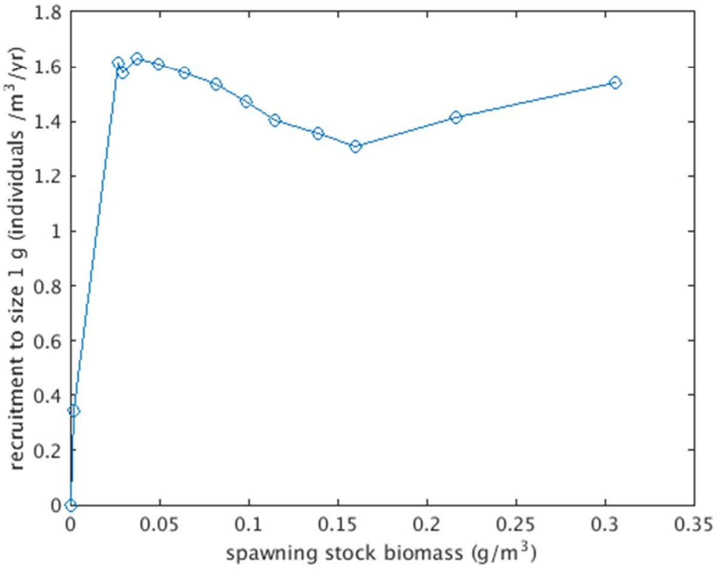


Figure S2. Relationship between spawning stock biomass and recruitment to size 1 g. Recruitment is calculated as the product of egg production and probability of survival to size 1 g and is a model output rather than an externally specified assumption. Each point on the graph represent a different number of fishers N_F in the agent-based fishing model: the right-most point is the unexploited state ($N_F = 0$) and increasing numbers of fishers reduces the spawning stock biomass.

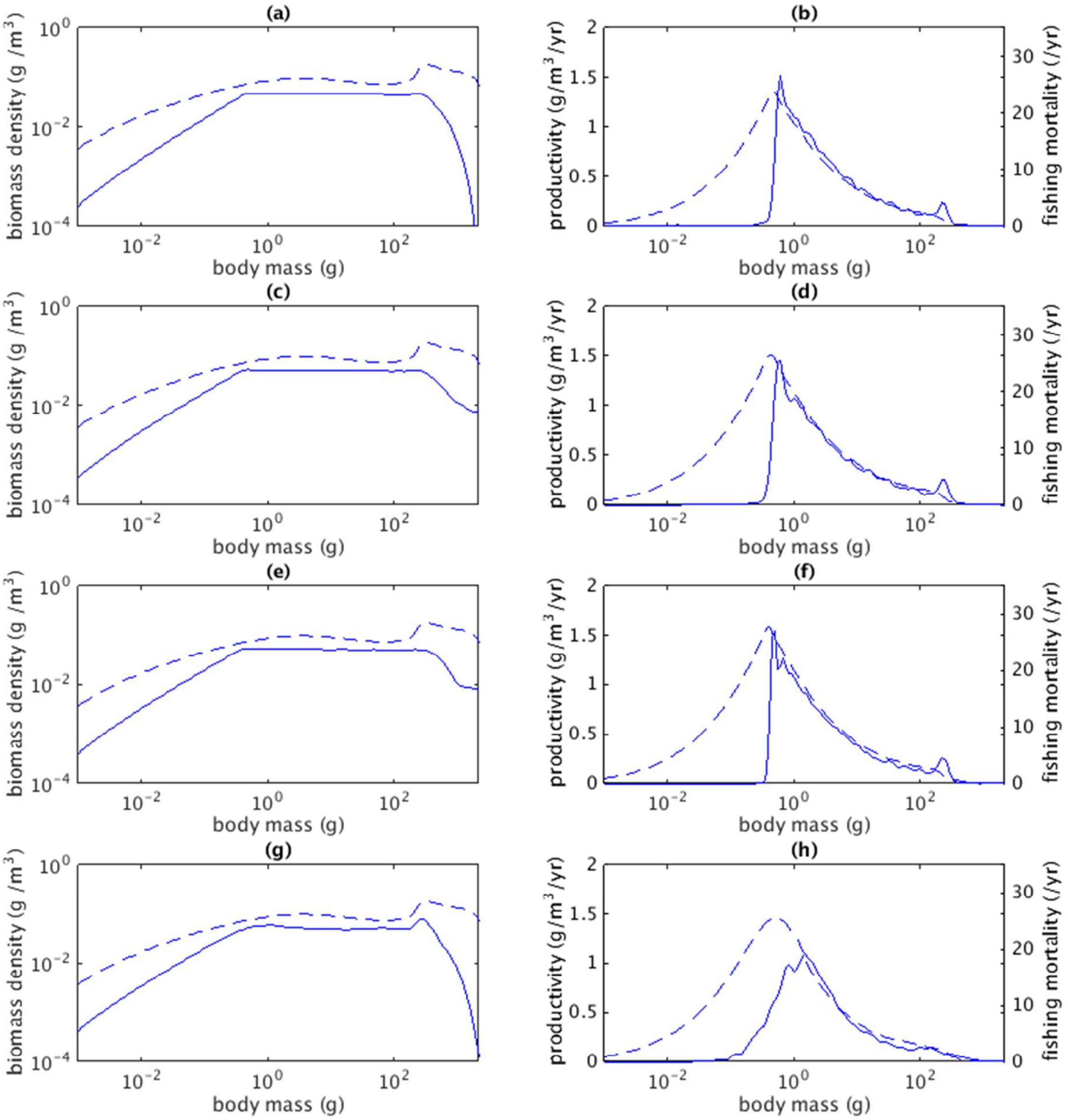


Figure S3. Simulation results for four alternative agent-based models for individual fisher behaviour given in Table S1. **(a,c,e,g)** Biomass spectrum of the unexploited (dashed) and exploited (solid) systems. **(b,d,f,h)** Productivity (dashed) and aggregate fishing mortality (solid) as a function of body mass. **(a,b)** Model 1. **(c,d)** Model 2**. (e,f)** Model 3. **(g,h)** Model 4. Results are shown with 6000 fishers after running the model for a total period 5 years. Parameter values as in Table 1.

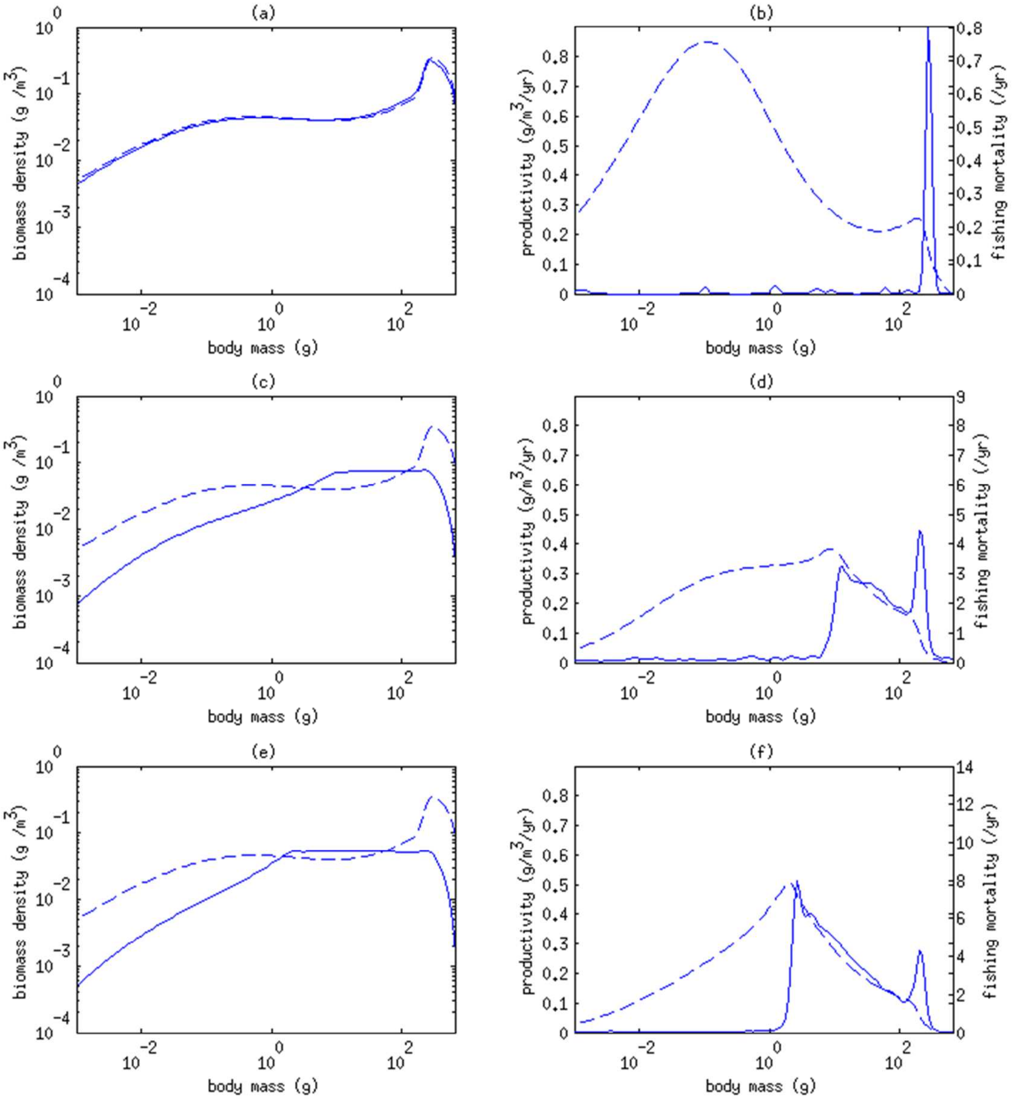


Figure S4. Simulation results for a different set of life history parameters representing Atlantic mackerel. **(a,c,e)** Biomass spectrum of the unexploited (dashed) and exploited (solid) systems. **(b,d,f)** Productivity (dashed) and aggregate fishing mortality (solid) as a function of body mass. Results shown are after running the model for a total period of 5 years with: **(a,b)** 100 fishers; **(c,d)** 4000 fishers; **(e,f)** 8000 fishers. Parameter values: $w_m = 200$ g, $w_\infty = 650$ g, $\beta = 6$, $u_0 = 100$ m^{-3}, $F_0 = 0.0025$ yr^{-1} ; other parameters as in Table 1.

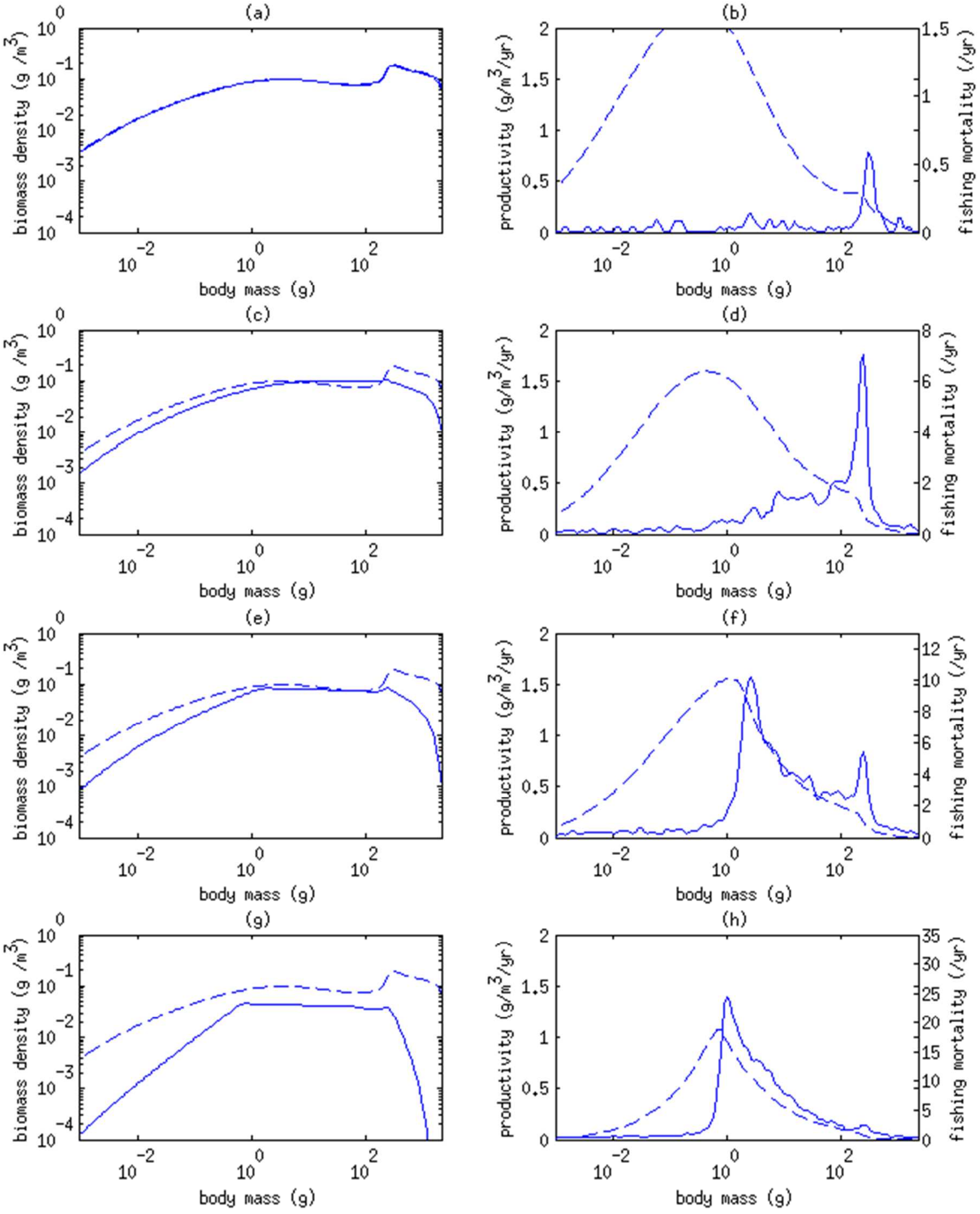


Figure S5. Simulation results with a longer period of time ($T_F = 60$ days) between changes in fishing gear. **(a,c,e)** Biomass spectrum of the unexploited (dashed) and exploited (solid) systems. **(b,d,f)** Productivity (dashed) and aggregate fishing mortality (solid) as a function of body mass. Results shown are after running the model for a total period of 5 years and for the same four levels of fishing pressure as in Fig. 1: **(a,b)** 75 fishers; **(c,d)** 1200 fishers; **(e,f)** 3000 fishers; **(g,h)** 6000 fishers. Other parameter values as in Table 1.

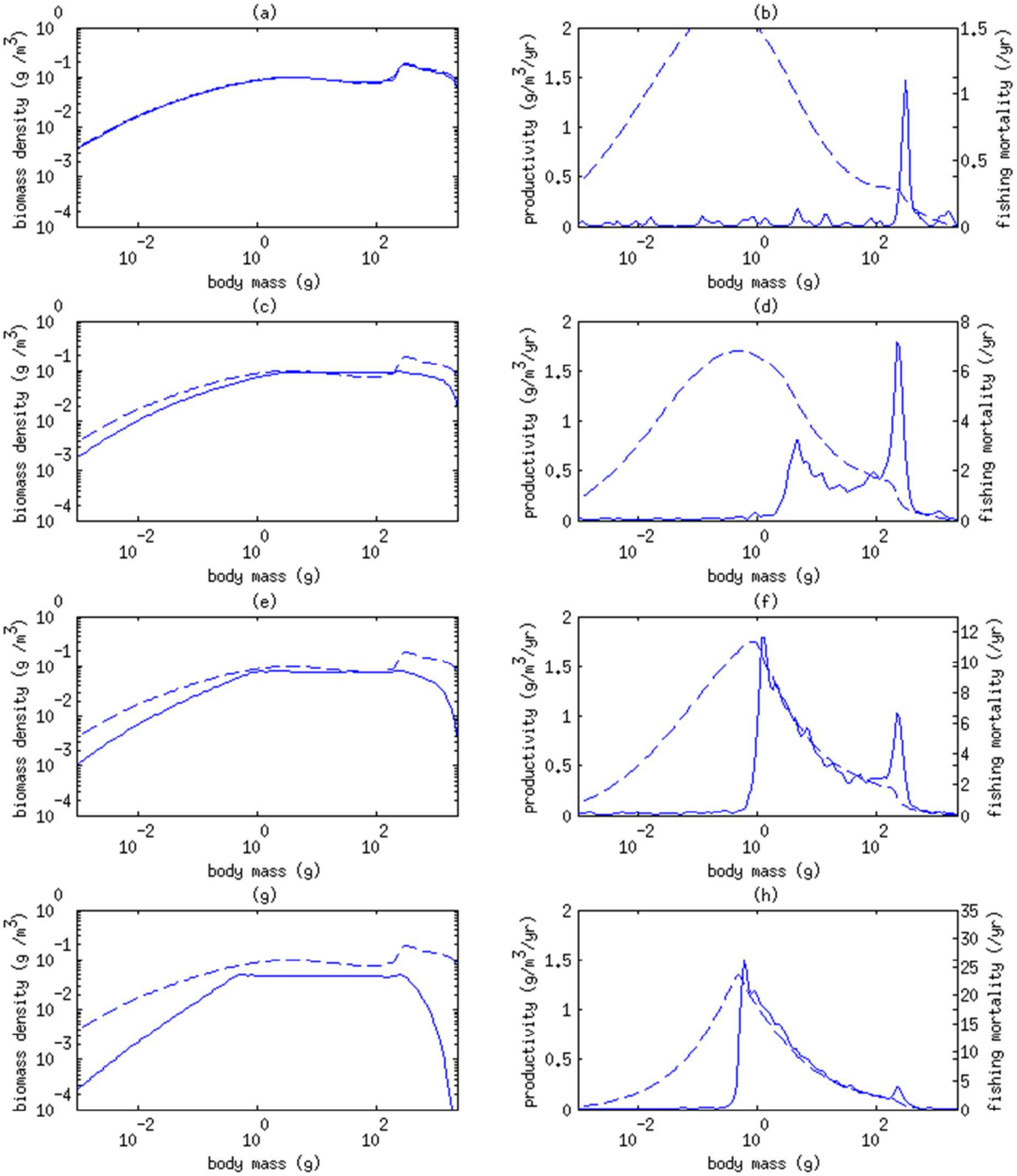


Figure S6. Simulation results with noise added to the individual fishers' mortality functions. **(a,c,e)** Biomass spectrum of the unexploited (dashed) and exploited (solid) systems. **(b,d,f)** Productivity (dashed) and aggregate fishing mortality (solid) as a function of body mass. Results shown are after running the model for a total period of 5 years and for the same four levels of fishing pressure as in Fig. 1: **(a,b)** 75 fishers; **(c,d)** 1200 fishers; **(e,f)** 3000 fishers; **(g,h)** 6000 fishers. Parameter values as in Table 1.

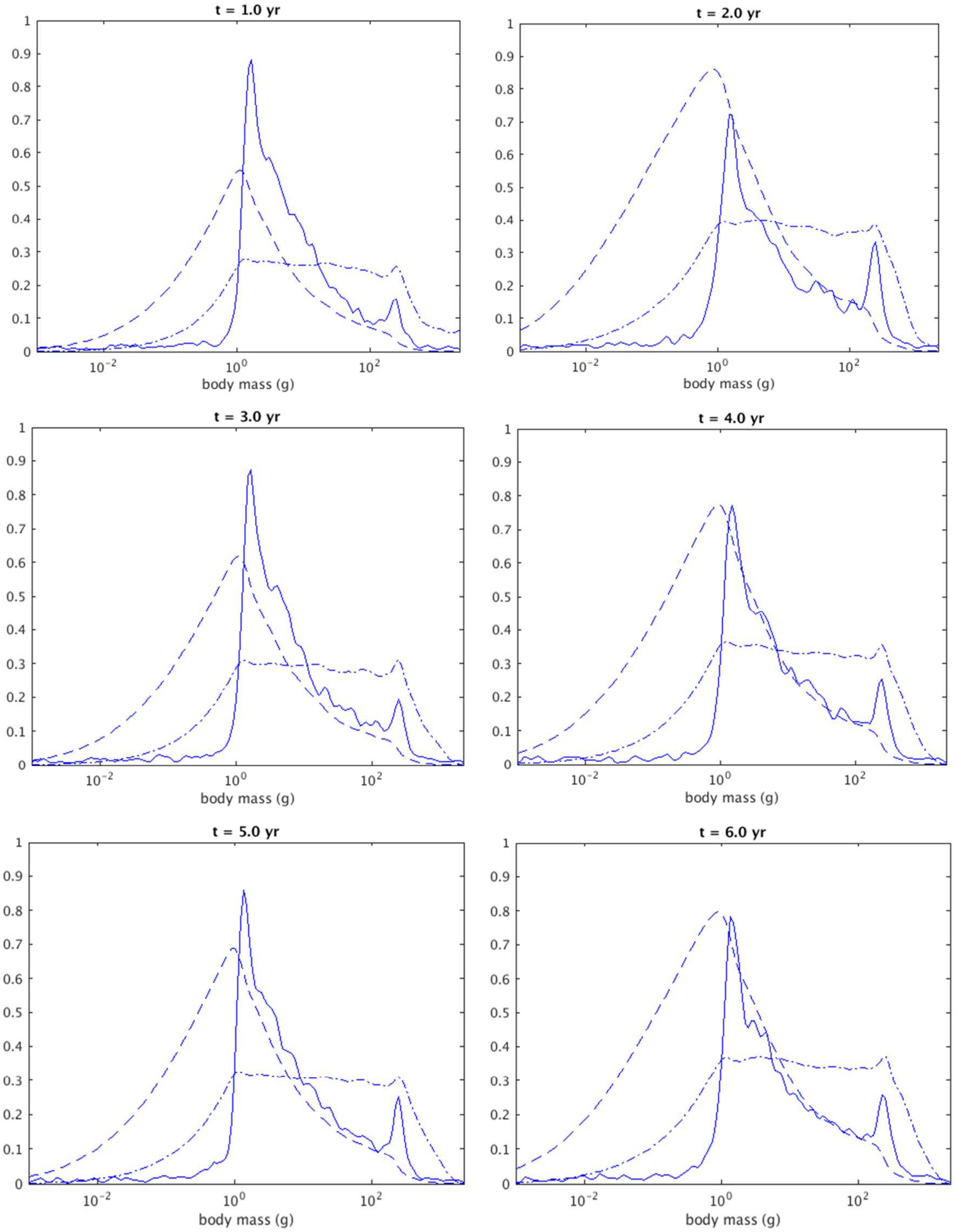


Figure S7. Simulation results with random yearly variations in reproduction. Biomass density (scaled by 0.2 g m^{-3}, dash-dot), productivity (scaled by 2 g m^{-3} yr^{-1}, dashed) and aggregate fishing mortality (scaled by 20 yr^{-1}, solid) shown at six different time points. Each year, the log of the reproduction parameter ε_0 was chosen to be a $N(\ln(0.5), 0.5)$ random variable. In this example, the values of ε_0 generated for the first 6 years were: 0.20, 0.76, 0.32, 0.53, 0.38, 0.58. Results shown with 4000 fishers. Parameter values as in Table 1.

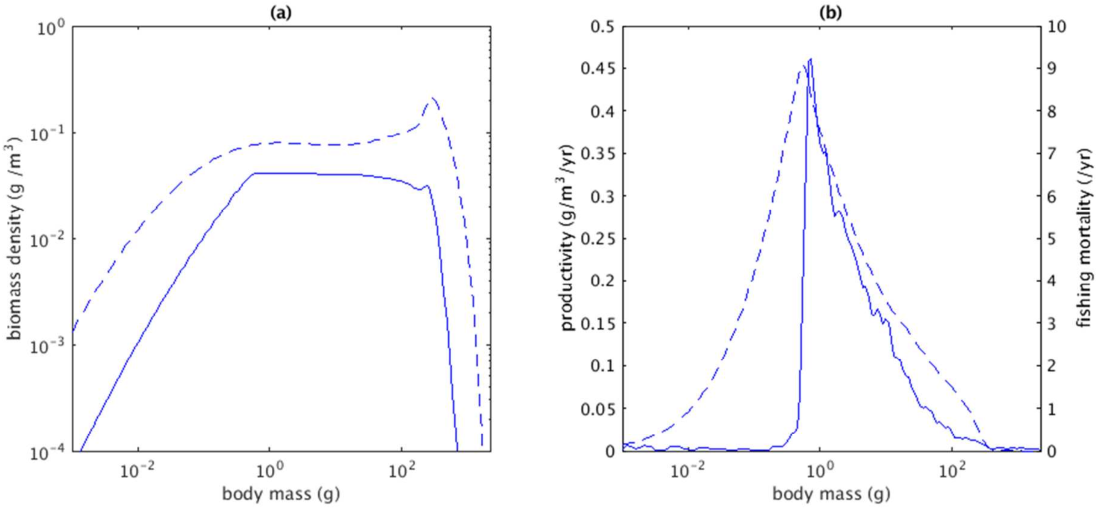


Figure S8. Simulation results with the fixed plankton spectrum replaced by a von Bertalanffy growth function. **(a)** Biomass spectrum of the unexploited (dashed) and exploited (solid) systems. **(b)** Productivity (dashed) and aggregate fishing mortality (solid) as a function of body mass. Results shown are after running the model for a total period of 5 years with 2000 fishers. Predator search rate $A = 375$ m^3 g^{-a} yr^{-1}, intrinsic mortality rate $\mu_0 = 0.4$ yr^{-1}; other parameter values as in Table 1.

Dear Professor Hart

Thank you for your message regarding our manuscript ID FaF-16-Feb-OA-032 and for the opportunity to resubmit a revised version.

We have substantially revised the manuscript in response to the issues raised by the two reviewers, and we have included a detailed point-by-point response to their comments below. In the revised manuscript, we have marked substantial changes from the previous version in bold, blue text.

We hope that you now find the manuscript acceptable for publication in Fish and Fisheries. We look forward to hearing from you.

Yours sincerely

Michael Plank.

Reviewer: 1

Background:

BH is a potential alternate harvesting strategy to current fisheries management that incorporates ecosystem considerations, and has been demonstrated to give high yield in biomass (though not necessarily in value) with low ecosystem impacts in small-scale subsistence fisheries, and simplified models. The models also suggest that under a BH regime the stocks are better able to resist overfishing. The remaining scientific questions are around the importance of natural variability, the science demands of such management, and the enforcement techniques required. There is an additional question around the aim of a fishery (yield in biomass or profits, value or employment), but that is more a political and social issue than a scientific one.

Summary:

The question raised in the introduction (and implied by the title), namely how can balanced fishing patterns arise in large-scale oceanic commercial fisheries, is of high interest in current fisheries management and research. However the paper does not address this large and important question, but rather the much more limited question of how BH could arise in a small-scale non-commercial fishery (where it has already been shown to arise in a real world example). This is discussed in the text (where the authors state that this work is a first step), however the title and to some extent the introduction are misleading, promising much more than the paper delivers. In a sense the idea that fishers free to target any size category and with no economic constraints should operate in proportion to the available biomass is trivially obvious, and as I outline below this does not automatically equate to BH. The importance of the work is to produce a model which can attempt to model fishing patterns that could lead to BH in a small scale non commercial setting – and this is an important necessary precursor to investigating a more commercial and large scale setting.

We have changed the title by adding the words "in small-scale fisheries" to make the scope of our results clearer and avoid misleading the reader. We have also edited the Introduction by qualifying that our results apply to small-scale fisheries in several places (lines 59, 94, 138). We don't agree that questions about small-scale fisheries are less important or more limited than large, commercial fisheries. 90% of the world's fishers are in small-scale fisheries and these contribute around 75% of the global catch for human consumption. We have pointed out the importance of small-scale fisheries on lines 64-66 with some supporting references.

We do agree that modelling fishing patterns that could lead to BH in a small-scale setting is a useful stepping stone towards investigating BH in a commercial setting and we have added some text around this in the Intro (lines 77-78).

We don't agree the results about how fishers free to target any size category will operate is trivial. Most fisheries models include an externally specified fishing mortality and size selectivity curve. Very few if any models have investigated how mortality and size selectivity emerge from the aggregate behaviour of independent individuals. The key result of our paper, that the emergent fishing mortality is closely matched to productivity across sizes, is completely novel.

There is a critical issue over the way recruitment is modeled, which makes me worry that results obtained may be an artifact of a model oversimplification. The key result is that the unfished biomass density curve is flat topped, and remains so after the "free choice" fishing, which is interpreted as the fishing being balanced. However it may simply be that the fishing model acts to flatten out any peaks. Given the variability in recruitment of most marine fish stocks one would not, in general, expect a flat topped unfished biomass distribution. It is thus important to verify if the fishing is indeed balanced (preserves the shape of the curve at a lower level) or simply flattens out the curve (i.e. not balanced). I discuss this in more detail below, along with a test that the authors could perform to check what is going on.

We think the reviewer may have misunderstood a key point here. The unfished biomass density curve is NOT flat topped; our results is precisely that the fishing model acts to flatten out any peaks in the biomass density (dashed curves in Fig. 1 are not flat topped, but solid curves are). We have rewritten the relevant text to make this clear (lines 291-296). The definition of BH is NOT that the biomass density curve remains the same shape, but that fishing occurs in proportion to productivity (this is the standard definition of Garcia et al 2012). Thus, we make no inference from the biomass graphs in the left-hand column of Fig. 1 about whether fishing is balanced or not. But these graphs DO demonstrate our prediction of a Nash equilibrium, in which all fishers are obtaining the same catch because the biomass is the same at all targeted sizes. Our inference that fishing is balanced comes from the right-hand column of Fig. 1 where we see the emergent fishing mortality curves are closely matched with the productivity curves. Again, we have clarified the relevant text to make the logic of this argument clearer (line 304-306).

Regarding recruitment, almost any theoretical paper that includes a recruitment function (whatever its shape in terms of density dependence or not) has this 'fixed' and constant for simplicity, and does not include variability (unless recruitment variability is the specific objective of the investigation). The main caveat that we needed to make clear is that our model analysis concerns equilibrium behaviour. Clearly, real systems frequently do not operate at equilibrium due to a range of factors including environment variability. Nonetheless, equilibrium analysis is a powerful and widely used tool in many fisheries models that can give insight into the behaviour of

the system, without attempting to predict complex non-equilibrium dynamics. We have added some qualifying text about this (lines 72-74). We have added some caveats about the recruitment model and noted that it does not include environmental factors which can lead to a significant amount of year-by-year noise in the recruitment (lines 173-176).

In addition, we have added some results showing the effect of variable recruitment from year-to-year. To simulate this, every 1 yr we set the egg production parameter ε_0 to be a log-normally distributed random variable (which allows for occasional large recruitment years). The results are included in Supporting Information (Fig. S7) (following on from the result showing the effect of noise in fishing mortality) and referred to from the text line 353. As the graphs show, this causes additional noise in the productivity, biomass and fishing mortality and there is some variation from one year to the next. However, the qualitative result – that fishing causes the biomass density to be flattened and the fishing mortality is closely matched with productivity – is unchanged. This shows that the results are not an artefact of the stable recruitment model.

Many of simplifications are reasonable in a modeling context (e.g. the constant and equal effort of all fishers, single species model), and while the fishing selection model may be simple it seems effective and appropriate. The focus on fishing selection rather than overall effort is also valid, these are separate issues. However the recruitment simplification one is not reasonable in this context, for reasons discussed in detail below. The generality mentioned in the discussion for the modeling approach is valid (with the exception of the recruitment variations). The paper is generally well written, except for the disconnect between the "advertising" in the title (and to a lesser extent in the introduction) and the work presented, and the paper represents an important step forward in BH research.

We thank the reviewer for these positive comments.

Details:

Recruitment model:

In addition to the limited nature of the simulation, there is a second, potentially serious problem, which is not addressed in the paper. The recruitment model used is a linear function of adult biomass. This means that recruitment is, in a sense "stable" (not constant, but not varying except with the biomass distributions within this model).

The reviewer is correct that we are using a density-independent **reproduction function. Density dependence (e.g. Beverton & Holt or Ricker curves) are generally used because Y/R models do not have density dependence (DD) incorporated, so it has to be put in with a stock-recruitment curve. In the size-spectrum model, density-dependence acts via predation at all life stages and is not restricted only to an assumed stock-recruitment curve. In fact, if recruitment is as usual interpreted as survival to a specific age or size, then the size-spectrum model does have a density-dependent relationship between stock and **recruitment**, because survival depends on the density of predators. Recruitment is therefore not an external assumption, but is a model output. We have added text explaining this aspect of the model on lines 166-173. In addition, we have added a graph to supporting information (Fig. S2) to show the relationship of calculated recruitment with spawning stock biomass. This produces a familiar looking density-dependent curve, similar to a Beverton-Holt model.**

This does not at all reflect the case in most oceanic fish stocks, where recruitment is highly variable and driven by a range of (typically poorly understood) factors including small scale overlap with food, small scale overlap with predators, currents, temperature, salinity and more. The result is typically runs of years with poor to average recruitment with sporadic “good yearclasses”, up to an order of magnitude (or more) higher than the surrounding years. This simplification matters to question addressed here, and I suspect may have a high impact on their findings. If recruitment is a linear function of adult biomass one would expect an exponentially decaying number of fish by age in the unfished population, and it may be the case that growth would balance out mortality giving a “flat topped” biomass by size curve. However, in a typical fish stock this is not the case, rather there is a “bump” that propagates through the size distribution as a good yearclass grows and ages. This bump is not related to productivity at that size category, but to the historic factors at the smallest sizes that gave rise to the good yearclass. Hence fishing according the biomass and fishing according to the productivity become different. In a multispecies model one could argue that such bumps for individual species “average out” to a smooth curve, but this model is single species so that does not apply.

We agree that in reality environmental variability can cause large changes in the system over time. However, our recruitment model does NOT mean there is an an exponentially decaying number of fish by age in the unfished population. This is because the mortality rate is not assumed to be constant, but is dependent on predation mortality, which typically declines quite substantially with age. Thus there is no assumption, explicit or implicit, that growth balances mortality to give a flat-topped biomass. The flattening of the biomass spectrum seen in the results is a solely consequence of fishing, and emerges regardless of the precise rates of reproduction, growth and mortality. (See below for discussion on the effects of a strong yearclass).

My reading of their fisheries selection model is that fishermen actually target size categories based on the biomass at each size category. In a stable recruitment model this is also proportional to productivity (since both follow an exponential decay). However in a situation with good yearclasses this is no longer true – fishery can be either proportional to biomass at size OR to productivity at size of capture, since these are no longer related. It is therefore possible (even likely) that the results obtained are an artifact of the simplification on recruitment – the fishermen are simply flattening out whatever unfished curve exists, and this just happens to look like the unfished curve in this particular example. There is some hint of this in figure 5 where the slight peak in the large biomass is “fished down” to the flat curve.

The results are not an artefact of the model used for recruitment, as we have now shown with the additional results on variable recruitment. The recruitment model determines the abundance of fish of the smallest size in the model. What happens to these fish subsequently is purely determined by the amount of food available for them to grow, the number of predators that are eating them and the fishing mortality. Neither productivity nor biomass follow an exponential decay, and these two curves are not proportional. This is clear from Fig. 1 which shows that the biomass (left column) and productivity (right column, dashed curves) curves have quite different shapes and are not proportional to each other. Yes the fishers are flattening out whatever unfished curve exists – that is precisely the prediction of the Nash equilibrium – but this does NOT look like the unfished curve, which is not flat.

It should be relatively easy to test this. In addition to the current model runs, do a run in which a single large yearclass is artificially induced (say by a factor of 10). It is possible that the authors may also need to increase the frequency at which fishermen change size categories, since the model mechanism (in which fishermen have no advance knowledge of what size to fish) is likely to be relatively slow to converge and thus might or might not be fast enough to follow the "bump" if they fishermen do not resample often enough. In effect, the described Nash equilibrium is only valid for given model year, and will need to be recalculated each year as the yearclass propogates through the population. Such a test would identify if the fishers are following productivity (and thus BH) or biomass (and thus not, in general, BH). In this case a flat biomass spectrum would NOT indicate BH, since it would imply higher fishing pressure based on biomass distribution (not productivity distribution) to artificially create a flat size spectrum that was not present in the unfished stock. BH would be indicated by a preservation of the "bump", but at a lower level.

We have performed the test suggested by the reviewer. In fact, the dynamics are significantly more complex than the reviewer suggests due to interactions among yearclasses (which are typically not accounted for in Y/R models): the increased biomass in the good yearclass acts as a major food source for larger fish, meaning that they can grow faster and therefore have higher productivity. As the good yearclass grows, it inflicts higher predation mortality on its prey, which are subsequently depleted leading to reduced productivity. This leads to a number of peaks and troughs of varying sizes in the biomass curve. Nonetheless, the behaviour of the fishers "following the bump(s)" can be seen as an increase in fishing mortality that follows the high biomass size range. However, this high fishing mortality then reduces the yearclass back down to "normal" levels, and the system subsequently reconverges to the equilibrium state.

These results can be seen in the Figure appended at the end of this document. We have not included this in the paper because, as we have now explained, this is an equilibrium analysis and we believe a comprehensive analysis of non-equilibrium behaviour is beyond the scope of the current study. The reviewer is correct that the match between F and productivity is an equilibrium result and that F may be more influenced by biomass than by productivity when the system is away from equilibrium. As our results also show, when the fishing pressure is relatively low then fishing effort is concentrated on the size where the biomass is at its greatest (whether that is an equilibrium state or a bump in the biomass due to a good yearclass). There is clearly a complex interplay between biomass, productivity and time-dependent dynamics away from equilibrium that needs further investigation. However, this is beyond the scope of the current work. We have added a paragraph discussing these issues and clarifying the limitations of the equilibrium results (lines 382-389).

A separate issue with recruitment is that typical data from fisheries suggest that up to some SSB level there is a strong relationship between adult biomass and recruitment, but past that point the link to adult biomass disappears and only "environmental" factors matter. This is something that the authors should include in future models (as it would affect the absolute level of fishing a stock could withstand), but does not affect the findings here or the test described above.

We agree that incorporating a saturating stock-recruitment relationship, e.g. Beverton-Holt curve, into the model is something that could be looked at in the future, although as we now show (lines

168-173 and Fig. S2) model recruitment does have this type of relationship with SSB, but this is a model output rather than an assumption.

I am no expert on fresh water stocks. It may be that recruitment pattern presented here is valid in these cases – in which case the words "stable recruitment" should be added to the title and this limitation discussed in order to avoid giving the impression that the results are valid for typical marine stocks. In any case the test described above should be carried out in order to check if the fishermen are actually "doing BH" or not – even if the unfished biomass curve is unrealistic for this species the test is still a necessary diagnostic.

We have added clarifying statements that the results are for an equilibrium model (line 72-74 and 382-389), and that this effectively means stable recruitment (line 176). We prefer not to include this in the title as it would make it rather clumsy (and there are many examples of equilibrium models in fisheries science that do not explicitly include this word in the title).

Side note: recruitment can be modeled as a separate process or (as here) as a productivity on the youngest life stages. For these purposes it really doesn't matter if they boost the egg production or reduce mortality on the youngest life stages – the aim is not to realistically model the processes behind a large yearclass (which people have been failing to do for over a century), but rather to induce one and follow the effects as a diagnostic test.

We agree that either of these would be valid modifications to the recruitment model that could be tested. The results we have described here to have investigate variations to recruitment were obtained by changing egg production, rather than mortality on the youngest life stages.

Small-scale, non-commercial

On the other point, of simulating a small-scale non-commercial fishery, the authors do a good job of discussing the impact of price differentials. It would also be worth mentioning that cost of capture also varies (e.g. fishing adults on a spawning migration of demersal fish should give lower cost per kg than fishing on a mixed population spread over the feeding grounds). This means that even absent price differentials, there is likely to be an incentive to target some size categories. The authors should also note in the discussion that while oceanic fishermen have considerable freedom to change their size selection, this freedom is not absolute (a long line fisherman in the example above could target the adults on the spawning migration or the mixed population on the feeding grounds, but could not feasibly target the smallest individuals at any viable capture cost per kg).

We have added a comment that these differentials can arise from variations in the cost of capture as well as variations in the market price (line 404). We have also added a caveat that there are limits on the ability of fishers to change their size selection (line 478).

In addition to the above test being necessary, I would also strongly recommend that the words "small-scale, non-commercial" be added to the title to avoid the current misleading impression currently being given.

We have added the words "small-scale" to the title. We prefer to avoid using the word commercial as defining a commercial versus a non-commercial fishery in different environments is not straightforward. No fishery is completely non-commercial: fishing for just food is also a business-related activity in the sense that the fisher will chose how to invest his energy (labour).

Reviewer: 2

Comments to the Author

The paper investigates how fishing selectivity patterns can emerge on a single species, given that the fishermen chose to fish at the sizes that maximize their yield. The paper uses a previously published ecological model (with some slight parameter changes), and couple it with a simple model describing fisherman behavior. Balanced harvesting is generally a concept dealing with patterns on the entire ecosystem, but one of the big controversies is the call for fishing immature fish. This paper does not deal with this as such (as we already know from Law et al (2015), this particular model promotes fishing small fish for an increase in yield), but it implicitly becomes a large part of the ms as that particular ecological model prediction influences fisherman choice in the behavioral model.

The results presented in the ms are relevant and novel because it shows how a fishing pattern can emerge given some biological characteristics (i.e. the productivity) of the target species. What is not so novel about the results is that the fishing pattern (that maximizes yield) emerging is almost identical to the Law et al (2015) pattern, which was already shown to increase yield over a "flat" fishing pattern. This is an outcome of the assumptions given in this particular ecological model, and other models in fisheries science will often predict a different outcome (e.g. the "basic population model" mentioned by Froese et al. (2015).

We agree that other models predict a different relationship between productivity and body size and we have discussed this on lines 115-125. The novel result here, relative to the results in Law et al (2015) is not in the distribution of fishing mortality over body size per se, but the observation that the fishing mortality is proportional to productivity. This is a genuinely novel result: in Law et al, the fishing mortality was *specified* to be proportional to productivity, which in practice would require the productivity to be known and management steps taken to match fishing mortality with it; here the match *emerges* from the model as a consequence of selfish individuals' behaviour as opposed to any central management. We now explicitly point this out on lines 125-128. One of the strengths of this result is that it is not dependent on the specific choice of ecological model. If other models are correct and the productivity of large, mature fish is higher, then this would be reflected in the fishing mortality that would emerge from individual fishers' behaviour as we have modelled. This is discussed in lines 439-446.

The model applied in the ms assumes that all fish over a certain size can only grow by eating their conspecifics (cannibalism). This induces strong adult density dependence. On the contrary, another assumption is that the background spectrum (only up to 0.02 g) is constant, which makes it impossible for density dependence for small sizes to emerge (there is no food competition). Adult density dependence is very rarely observed in marine systems, whereas it has often been observed early in life making the generality of the results less significant. I am no expert in African Catfish, but

I find it unrealistic that the adults only grow from eating their offspring, as these species are usually generalists and feed on diverse diets (such as insects and birds, see e.g. fishbase).

We have now pointed out these assumptions of the size spectrum model explicitly and noted that they are the subject of debate and that alternative assumptions are possible (lines 115-123) However, we again emphasise that the result about the emergent match between fishing mortality and productivity does not depend on the assumptions about strong cannibalism or constant background spectrum. To help test the robustness of our results to the assumptions of ecological model, we ran a set of model simulations with the constant background spectrum replaced by a fixed von Bertalanffy growth function. Under this formulation, instead of

growth = growth from eating plankton + growth from eating smaller conspecifics,

we have

growth = 0.5*(VB growth rate) + 0.5*(growth from eating smaller conspecifics)

We also reduced the predation mortality by 0.5 and increased intrinsic natural mortality by a factor of 2. Overall, this shifts the model away from one where the dominant predation/growth mechanism is cannibalism to one that is a mixture of canniabilism (which is a function of population abundance) and fixed, density-independent growth and mortality.

We obtain a similar flattened biomass spectrum and a close match between fishing mortality and productivity. We have added this graph to Supplementary Information (Fig. S8), referred to from the main text (line 354). Many variations in assumptions are possible here and they cannot all be tested, but this backs up our point that the emergence of the Nash equilibrium is not tied to a specific ecological model.

African catfish are generalists, which includes a significant element of cannibalism. As we comment in the paper (lines 135 and 428-431), it would also be of interest to see what happens in a multi-species system in which the relative important of cannibalism decreases as fish are preying on several different species.

I believe this warrants rigorous discussion of 1) how the advanced complexity of the behavioral model is a novelty over the results found in Law et al (2015), and 2) how the assumptions in this model differ from assumptions commonly applied in models used in fisheries science and how they affect the results.

We have added some discussion of how the behavioural model provides novelty relative to Law et al (2015), (lines 125-128). We have also added a comment that it could be applied to any chosen model for the dynamics of the fish stock (line 237) and some text describing how the assumptions of the behavioural model differ from standard models in fisheries science (lines 209-211).

In conclusion, I believe that the ms should be accepted for major revisions given that the authors can adequately correspond to the concerns listed above and justify the novelty of adding the behavioral model compared to the results achieved in Law et al (2015). In that case I would look forward to reading the final version in FaF.

We thank the reviewer for these positive comments. We believe we have responded to the concerns listed, and we have justified the novelty of adding the behavioural model (lines 125-128).

Law et al (2015) effectively assumes perfect knowledge about stock productivity in achieving a fishing pattern that results in BH. This paper assumes no knowledge at all, other than a fisher knowing how their own catch compares to those of others in the fishery. This is particularly topical when some of the criticism against BH is that it will be difficult to achieve with imperfect knowledge of productivity.

Minor

In general I am not impressed with the structure of the ms; the introduction contains several sections that belong in the discussion (e.g. 63-75), the methods and results include several sections that belong in either introduction (e.g. l. 261-271) or discussion (e.g. l. 272-276). The discussion also includes some results (Figure 5). I appreciate the well written language in the ms, but even though this is a revised version, I still think the paper needs a significant rewrite and tightening of structure.

Regarding lines 63-75, we chose to put these in the Introduction to make sure that the limitations to our arguments were clear up front. Given the comments of both reviewers on the previous version, we wanted to be sure that we did not mislead the reader into thinking that our results are more general than they are. Hence, we prefer to keep these qualifying statements in the Introduction rather than moving them to the Discussion.

We have now moved lines 261-271 to the Introduction. We have reduced the text previously on lines 272-276 to a single, short sentence (now line 281) as this issue is covered in more depth in the Discussion section. In the previous revision, we moved Fig. 5 to the discussion section to make clear that it is separate from the results of the model on not directly comparable to them, as the reviewers pointed out.

l. 335: I appreciate the sensitivity to model assumptions. But why not test any of the assumptions in the ecological model (e.g. constant background spectrum, all food over a certain size is acquired by cannibalism).

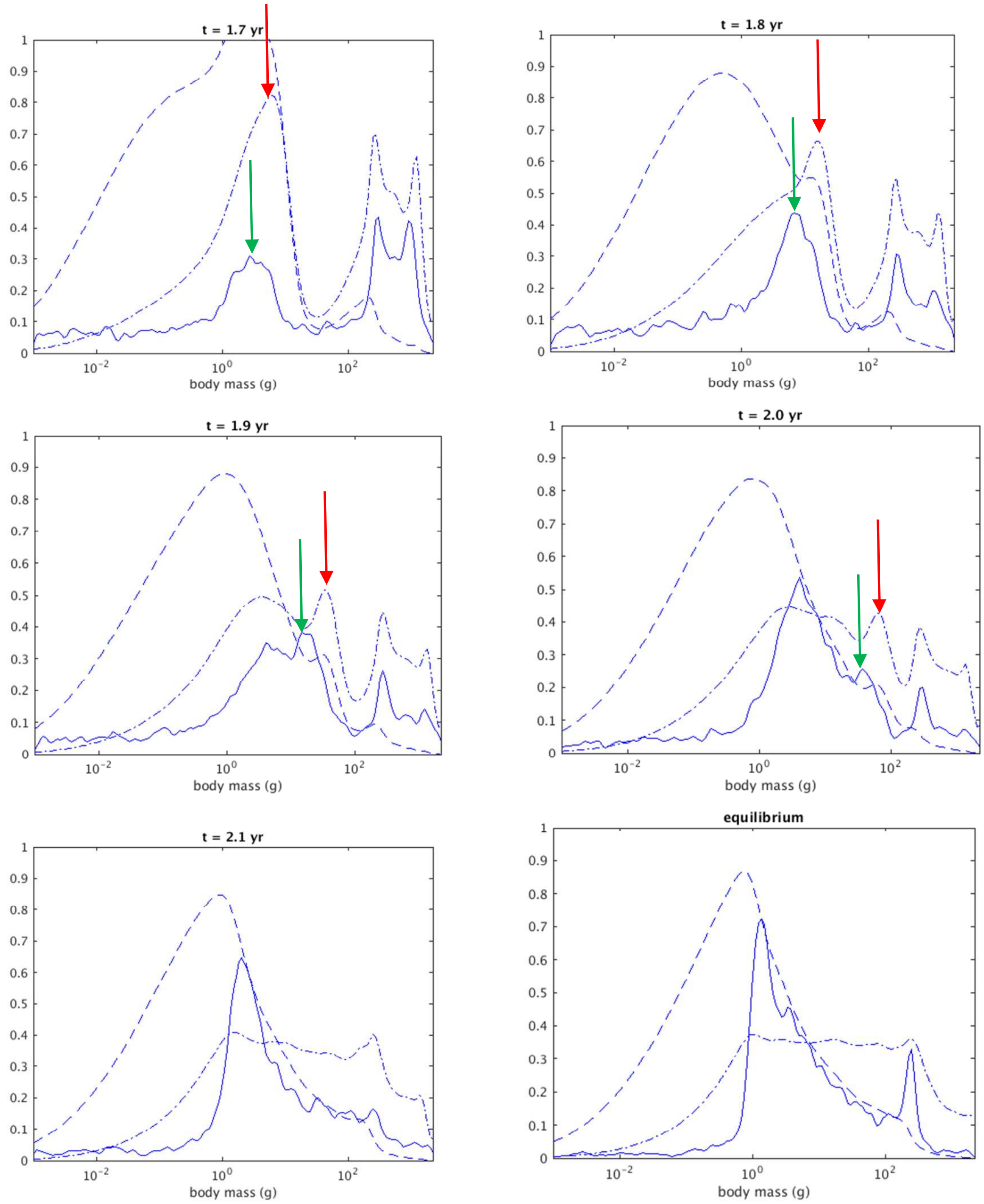
As described above, we have now added some results (Fig. S8) testing the ecological model assumptions about the growth rate and reducing the importance of cannibalism relative to an externally specified, density-independent growth.

Figure 1: Would the authors suggest to fish with a fishing mortality of 30 yr^(-1) (!!) on 1 g fish to maximize yield? It seems rather extreme, and probably an artifact of some rates in the model (which I suspect doesn't change the equilibrium result anyway). This warrants an explanation at least.

We have added to qualifying text to make it clear that we are not suggesting this would be a good idea as this level of fishing pressure would be a very dangerous place for the fishery to operate (lines 329-333). This is to the right of the maximum in the yield curve in Fig. 4 and close to the point at which the stock collapses. As a side note, the species modelled is a relatively fast growing (von Bertalanffy k=0.51 /yr); slower growing species would support a substantially lower fishing mortality (lines 190-193).

Figure 5: I have a hard time understanding how this figure fits into the ms. Since the Celtic Sea has a catch of species with different asymptotic size than African Catfish, it is expected that the relative catch will have a different size composition.

As commented above, Fig. 5 is separate from the model and not directly comparable to model results. In fact the Bangweulu data in Fig. 5 is not just catfish but includes several different species. The Celtic Sea data also includes several different species, all of which different asymptotic sizes. What is most interesting about Fig. 5 is that, although the fisheries display similar catch characteristics at large sizes, the Bangweulu fishery catches fish down to significantly smaller sizes than the Celtic Sea. This is not model validation, but it is consistent with the model results that individual agents in a small-scale fishery will target small fish and that, as long as overall fishing pressure is not too high, this can be sustainable.



Non-equilibrium dynamics resulting from the occurrence of a period of high reproduction. Egg production was inflated by a factor of 100 between t = 1 yr and t = 1.5 yr. Graphs show fishing mortality F (solid), productivity (dashed) and biomass density (dash-dot) as a function of body mass w. To plot all 3 curves on one graph, F is scaled by 20 /yr, productivity by 2 g/m3/yr and biomass by 0.2 g/m3. At t = 1.7 yr, the “strong yearclass” can be seen as a peak in the biomass curve (red arrow)and there is a corresponding peak in F (green arrow). At t = 1.8, the yearclass has grown slightly larger and the peak in F has followed it, though it lags slightly behind the biomass peak as it takes time for the fishers to respond to changing catches. Over time, the biomass of the strong yearclass is reduced by fishing and the system gradually evolves back towards the equilibrium state, where the biomass is flat topped and F is closely matched to productivity.