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

Michael J Plank[1,2], Jeppe Kolding[3,4], Richard Law[5], Hans D Gerritsen[6] & David Reid[6]

[1]School of Mathematics and Statistics, University of Canterbury, Christchurch 8140, New Zealand; [2]Te Pūnaha Matatini, a New Zealand Centre of Research Excellence, Auckland, New Zealand; [3]Department of Biology, High Technology Center, University of Bergen, PO Box 7800, Bergen N-5020, Norway; [4]Hjort Centre for Marine Ecosystem Dynamics, Bergen 5817, Norway; [5]York Centre for Complex Systems Analysis, University of York, York YO10 5GE, UK; [6]Marine Institute, Rinville, Oranmore, Co Galway, Ireland

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 criticized 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.

Correspondence:
Michael J Plank School of Mathematics and Statistics, University of Canterbury, Christchurch 8140, New Zealand
Tel.: +64 3 3642699
Fax: +64 3 3642587
E-mail: michael.plank@canterbury.ac.nz

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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 micromanagement. 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 article 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 maximizing 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 are 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 micromanagement, 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. As the Nash equilibrium is an idealized 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 theoretic 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, 2016a; Andersen et al. 2016). 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 multispecies 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:

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

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 Equation (1), $g(x, t)$ and $\mu(x, t)$

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:

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

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

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), that is, 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 internalizes 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 (Equation 2) and increased starvation mortality (Eq. S6). Conversely, if predators become depleted, their prey experience a release from predation mortality (Equation 3). For a full derivation of the size-spectrum model, see Law *et al.* (2015b). We parameterize 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:

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

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

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 $a = 0.008$ 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 m^3 g$^{-\alpha}$ year^{-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 year^{-1}
ξ	Exponent for intrinsic (non-predation) mortality	0.15
$w_{0,max}$	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

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:

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

This defines the $F(x)$ that is used in Equation (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 *i*th 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 $w_0 e^x$:

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

After every time period T_F, the *i*th 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; and 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 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 initialized 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 Equation (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 Equation (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 Equations (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 $F_0 = 0.01$ yr^{-1} constant. However, the results are similar if F_0 is increased with N_F held constant.

Results

Theoretic 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 (1–300 g), with
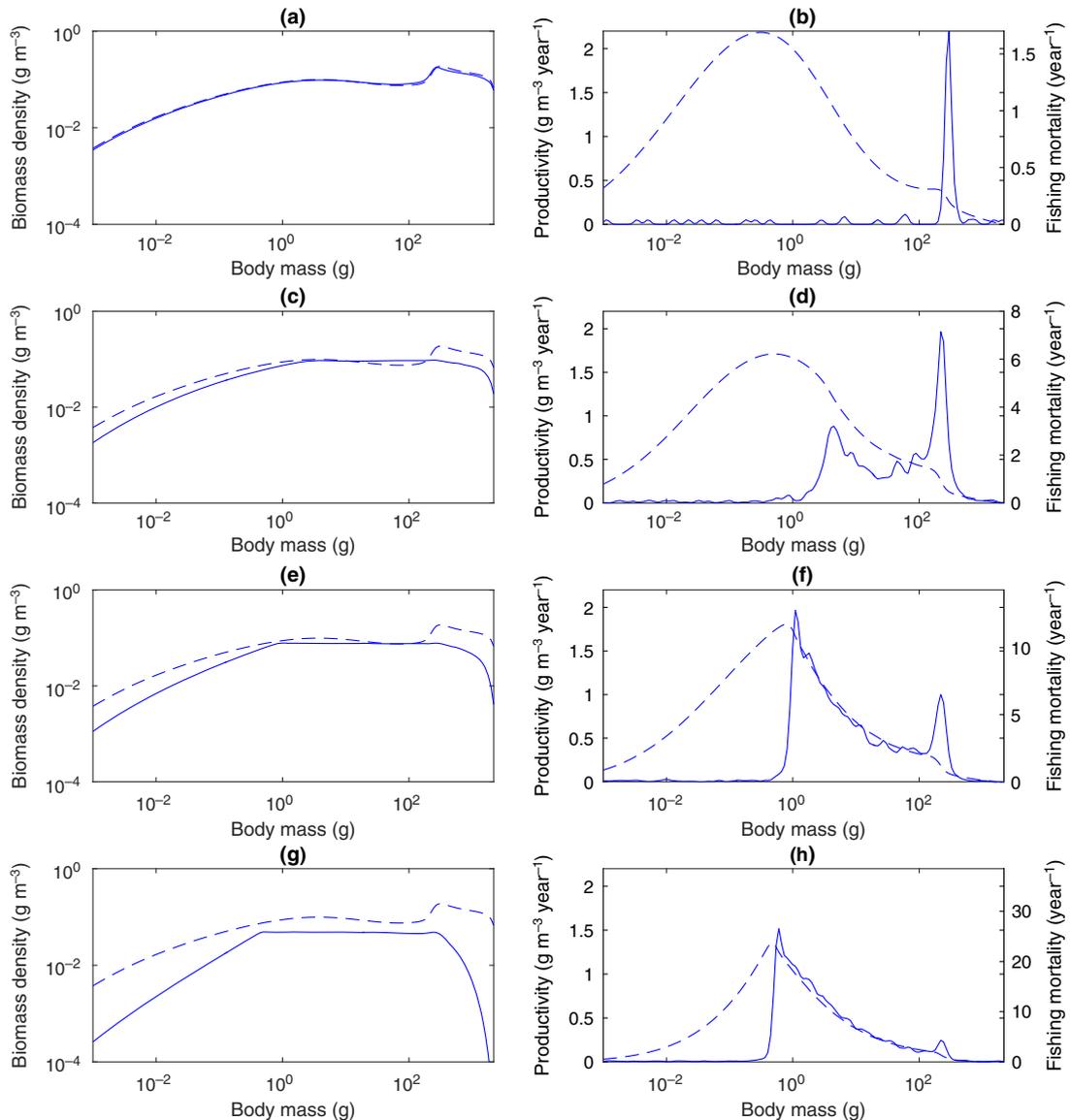
Figure 1 Simulated fishers without size regulations self-organize to produce a flat biomass spectrum and an aggregate fishing mortality that is proportional to productivity. (a,c,e,g) Biomass spectrum of the unexploited (dashed) and exploited (solid) systems. (b,d,f,h) Productivity (dashed) and aggregate 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. [Color figure can be viewed at wileyonlinelibrary.com]

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 1–300 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 (e.g. the example with 6000 fishers shown in Fig. 1g,h is a very
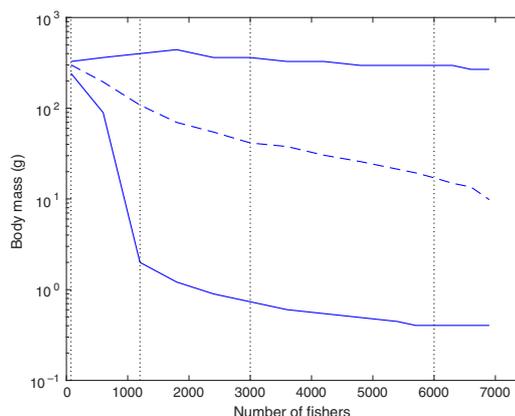

Figure 2 Increasing the number of simulated fishers without size-based restrictions results in smaller fish being caught. Number of fishers against the mean size of fish in the catch (dashed) and the body size range over which the biomass spectrum is approximately flat (the two solid curves show the 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 four fishing intensities as shown in Fig. 1. [Color figure can be viewed at wileyonlinelibrary.com]

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 occurs 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.
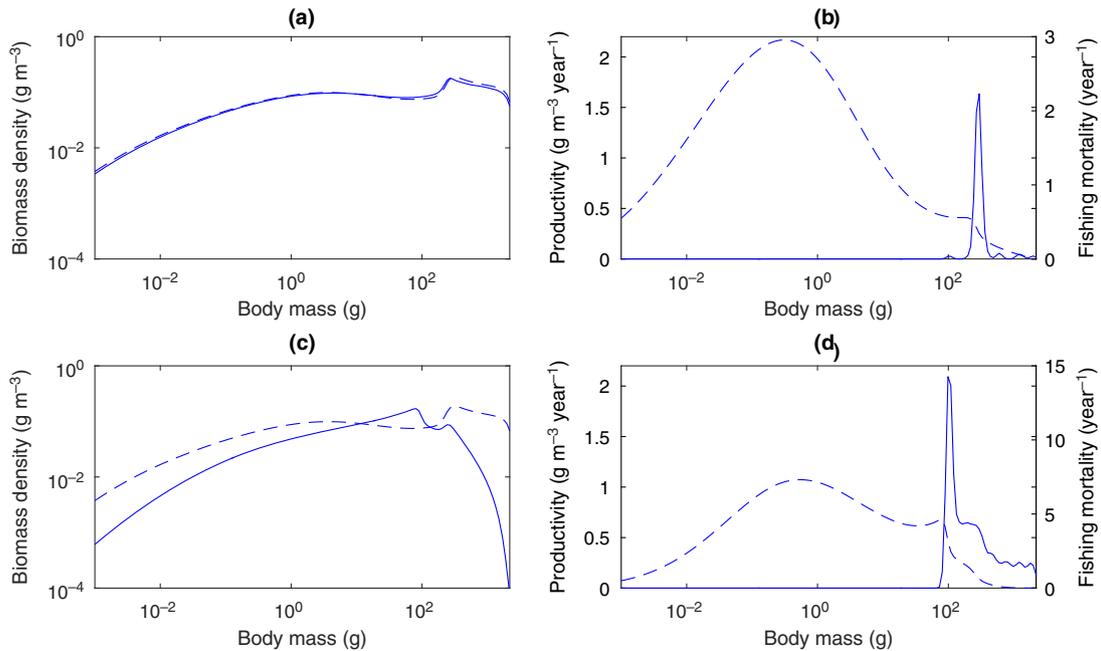
Figure 3 Simulated fishers operating under a minimum size regulation target fish close to the minimum allowed size. (a,c) Biomass spectrum of the unexploited (dashed) and exploited (solid) systems. (b,d) Productivity (dashed) and aggregate fishing mortality (solid) as a function of body mass. (a,b) 75 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. [Color figure can be viewed at wileyonlinelibrary.com]

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 parameterized 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, 2016b). Among the criticisms of BH are that it would require an impractical and level of micromanagement (Andersen *et al.*, 2016; Reid *et al.*, 2016) 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 maximize 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
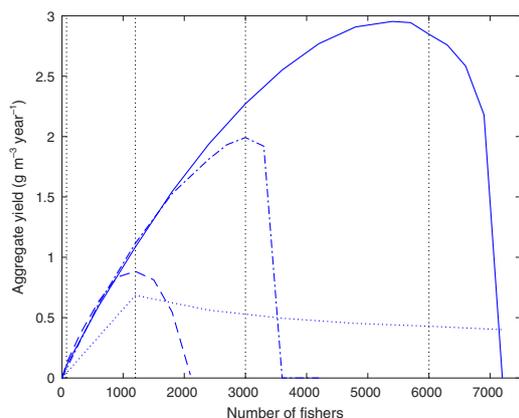
Figure 4 Imposing minimum size regulations on the simulated fishers reduces aggregate yield and can cause stock collapse at lower fishing pressure. Number of fishers against: sustainable aggregate biomass yield without size-based restrictions (solid) and with a minimum target size of 10 g (dash-dot), 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 four fishing intensities as shown in Fig. 1. [Color figure can be viewed at wileyonlinelibrary.com]

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 gill-net mesh size. These models do not accurately replicate the dynamics of a multispecies 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 maximize 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 organization 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 multispecies 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); and (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 recognize that increasing levels of fishing pressure will change the relative productivities of different body sizes (as shown, 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
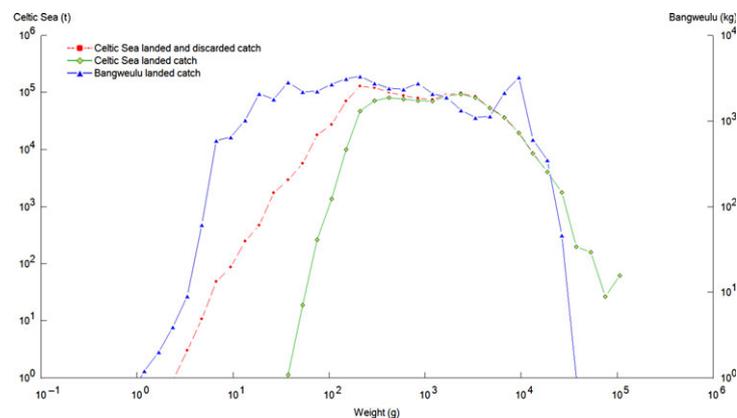

Figure 5 Empirical yield spectra from the Bangweulu Swamps and the Celtic Sea. Yield spectra calculated from catch data disaggregated by body mass from a small-scale fishery without size-based regulations in the Bangweulu Swamps (blue) and a highly regulated commercial fishery in the Celtic Sea (landings, green and landings+discards, red). [Color figure can be viewed at wileyonlinelibrary.com]

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 maximization 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 makes 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 as 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 organizing principle in which fishing effort tends to becomes distributed over body size in such a way as to equalize returns from targeting different sizes.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Definition of alternative agent-based models for fishers' choice of target size.

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 $w = w_\infty (1 - e^{-k(t-t_0)})^b$ (dotted) with $k = 0.51$ year^{-1}, $w_\infty = 2290$ g, $b = 2.983$, $t_0 = -0.5$ year (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.

Figure S3. Simulation results for four alternative agent-based models for individual fisher behaviour given in Table S1.

Figure S4. Simulation results for a different set of life history parameters representing Atlantic mackerel.

Figure S5. Simulation results with a longer period of time ($T_F = 60$ days) between changes in fishing gear.

Figure S6. Simulation results with noise added to the individual fishers' mortality functions.

Figure S7. Simulation results with random yearly variations in reproduction.

Figure S8. Simulation results with the fixed plankton spectrum replaced by a von Bertalanffy growth function.