

# Balanced harvesting is the bioeconomic equilibrium of a size-structured Beverton-Holt model

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## Abstract

Balanced harvesting was introduced as an alternative strategy to size-at-entry fishing with the aim of maintaining ecosystem structure and functioning. Balanced harvesting has been criticised on a number of grounds, including that it would require an infeasible level of micromanagement and enforcement. Recent results from a size-spectrum model show that the distribution of fishing mortality across body sizes that emerges from the behaviour of a large number of fishing agents corresponds to balanced harvesting in a single species. Size-spectrum models differ from classical size-structured models used in fisheries as they are based on a bookkeeping of biomass transfer from prey to predator rather than a von Bertalanffy growth model. Here we investigate a classical Beverton-Holt model coupled with the Gordon-Schaefer harvesting model extended to allow for differential fishing pressure at different body sizes. This models an open-access fishery in which individual fishing agents act to maximise their own economic return. We show that the equilibrium of the harvesting model produces an aggregate fishing mortality that is closely matched to the production at different body sizes, in other words balanced harvesting of a single species. These results have significant implications because they show that the robustness of balanced harvesting does not depend on arguments about the relative production levels of small versus large fish.

**Keywords:** gillnet fishing; Gordon-Schaefer model; Nash equilibrium; production; size-selectivity; small-scale fisheries

# 1 Introduction

Size-structured models are a standard tool in fisheries science for determining the sizes of fish to target and the overall level of fishing mortality, and date back to Beverton and Holt (1957). The size-at-entry is typically set at a level which prevents harvesting of fish: (i) which have not yet had chance to reproduce (termed recruitment overfishing); (ii) which have not yet reached their full growth potential (termed growth overfishing) (Sparre and Venema, 1989). The level of fishing mortality is set at or below the level that produces the maximum sustainable yield (MSY). This calculation typically relies on an assumed stock-recruitment relationship that specifies the number of new recruits for a given spawning stock biomass (Beverton and Holt, 1957; Ricker, 1954).

Drawbacks to selectively targeting large fish include destabilisation of fish stocks due to truncation of age structure (Hsieh et al., 2010), impaired recruitment due to the loss of large female mega-spawners (Hixon et al., 2014), and fisheries-induced evolution (Laugen et al., 2014). Balanced harvesting (BH) has been suggested as an alternative strategy, defined as *distributing a moderate mortality from fishing 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, 2015). In this definition, productivity was taken to mean “the amount of new organic matter produced per biomass unit”, with dimensions per unit time (Garcia et al., 2012). However, subsequent modelling studies (Law et al., 2012, 2016) defined productivity as the gross amount of biomass produced, which is usually termed production in the fisheries literature (e.g. Christensen and Pauly, 1992) and has dimensions mass per unit time. We adopt the interpretation of BH by Law et al. (2012) and define BH as a fishing mortality that is proportional to production in the rest of this paper.

There are two main facets to BH: (i) how fishing pressure is distributed over species; (ii) how fishing pressure is distributed over body sizes (Garcia et al., 2012). This paper is concerned with the second of these. Numerous studies have investigated the effect of different distributions of fishing mortality over sizes. The yield per recruit is maximised when fishing mortality is concentrated at the size at which the biomass of an unexploited cohort peaks, denoted  $l_{\text{opt}}$  (Beverton and Holt, 1957; Beddington and Kirkwood, 2005). However, catching fish of a unique size is clearly impractical in reality. Instead, mass-specific fishing mortality is commonly modelled as a size-selectivity function, for example a knife-edge or an S-shaped curve representing a trawl fishery (Sparre and Venema, 1989; Millar, 1992; Froese et al., 2016) or a dome-shaped curve representing a gillnet or longline fishery (Millar and Holst, 1997; Kolding et al., 2015). This allows parameters of the size-selectivity curve, such as the size at first capture, to be optimised. For example, Froese et al. (2016) suggested that the size at first capture should be set smaller than  $l_{\text{opt}}$ , such that  $l_{\text{opt}}$  is mean, rather than the minimum, size of fish in the catch.

69 The preceding examples all use a top-down approach, concerned with optimising a  
70 given pattern of fishing mortality determined by management. An alternative, bottom-up  
71 approach is to ask what pattern of fishing emerges as a result of decisions by multiple  
72 fishing agents, in response to economic or other drivers, about where and how to invest  
73 their fishing resources. Such studies have investigated the distribution of fishing effort  
74 across space, stocks or fishing technologies (Gillis et al., 1993; Gillis and van der Lee,  
75 2012; van Putten et al., 2012; Burgess, 2015). This approach has also been applied to  
76 the distribution of aggregate fishing effort of size or age classes that emerges from the  
77 size-selectivity of multiple fishing agents (Tahvonen, 2009; Ravn-Jonsen, 2011; Quaar  
78 et al., 2013). Diekert (2012) showed that, if individual fishers can target fish of any size  
79 of their choosing, economic returns are equalised across size classes and are much lower  
80 than in a managed fishery (i.e. a monopoly scenario). Plank et al. (2016) showed that, in  
81 such circumstances, the emergent fishing mortality is closely matched to the production  
82 of fish of different sizes – in other words, balanced harvesting – and that fishers avoid  
83 catching fish smaller than  $l_{\text{opt}}$  as it is economically unattractive to do so. The result of  
84 Plank et al. (2016) was demonstrated using a size-spectrum model, which is based on  
85 a bookkeeping of the biomass flows from prey to predator and from parent to offspring  
86 (Benoît and Rochet, 2004; Andersen and Beyer, 2006). The size-spectrum model used  
87 by (Plank et al., 2016) predicts that the peak in production, and therefore  $l_{\text{opt}}$ , occurs at  
88 relatively small body sizes. This prediction is controversial and is rightly being subjected  
89 to scrutiny (Froese et al., 2015, 2016; Andersen et al., 2016).

90 Importantly, however, the prediction that individual fishers will self-organise so that  
91 their aggregate fishing mortality is proportional to production stems from a model for  
92 fishers' choice of target fish size. Equilibrium is reached when no individual can increase  
93 his/her catch by switching to a different target size. This concept is not limited to size-  
94 spectrum models, but is applicable to any size-structured population model. Here, we test  
95 this prediction using a classical Beverton-Holt model for a single species. We show that  
96 the distribution of fishing mortality over size that emerges as a result of fishers attempting  
97 to maximise their own net profits is still closely matched to production. This is important  
98 because it means that the second facet of BH – the distribution of fishing pressure over  
99 body sizes within a species – is a robust, emergent outcome of fishers choosing what size  
100 fish to target, regardless of the relationship between production and body size.

## 101 2 Bioeconomic model

102 We use a bioeconomic model consisting of three submodels: (i) a model for the ecological  
103 dynamics of the fish population, structured by body mass; (ii) a harvesting model de-  
104 scribing how the level of fishing effort and its distribution over body mass changes with  
105 time; (iii) a stock-recruitment relationship.

## 2.1 Size-structured population model

We use the McKendrick-von Foerster partial differential equation (McKendrick, 1925; von Foerster, 1959) for the density  $n(w, t)$  of individuals of body mass  $w$ .

$$\frac{\partial}{\partial t} n(w, t) = -\frac{\partial}{\partial w} (G(w)n(w, t)) - (\mu(w) + F(w, t)) n(w, t), \quad (1)$$

This is a size-structured model for a population with growth rate  $G(w)$ , natural mortality rate  $\mu(w)$  and harvesting mortality  $F(w, t)$  at body mass  $w$  and time  $t$ . Eq. (1) is equivalent to a Beverton-Holt model (Beverton and Holt, 1957; Sparre and Venema, 1989) (see Supplementary Material, section 1 for details).

The analysis that follows is applicable with any growth and natural mortality functions. However, for the purposes of presenting numerical results, we use a von Bertalanffy (1957) growth model, for which the growth rate (in mass per unit time) at body mass  $w$  is

$$G(w) = bKw \left( \left( \frac{w}{w_\infty} \right)^{-1/b} - 1 \right), \quad (2)$$

where  $w_\infty$  is the asymptotic body mass,  $K$  is the von Bertalanffy growth parameter and  $b \approx 3$  is the exponent relating length  $l$  to mass  $w$  via  $w \propto l^b$ . The von Bertalanffy growth model is commonly used to describe size-at-age in fish populations and estimates are available for the growth parameter  $K$  and asymptotic mass  $w_\infty$  for a wide variety of species, see for example Fishbase ([www.fishbase.org](http://www.fishbase.org)). For the natural mortality rate, we use a function that scales allometrically with body mass (Andersen and Beyer, 2015):

$$\mu(w) = \mu_m \left( \frac{w}{w_\infty} \right)^{-\rho}, \quad (3)$$

The fishing mortality  $F(w)$  is described by a harvesting model, which we describe in the Sec. 2.2; the boundary condition for Eq. (1) at mass-at-birth  $w = w_0$  is given by a stock-recruitment relationship, which we describe in Sec. 2.3.

## 2.2 Harvesting model

The classical Gordon-Schaefer bioeconomic model (Gordon, 1954; Schaefer, 1954) describes the fishing effort on an unstructured population. Here, we extend the Gordon-Schaefer model to allow the fishing effort  $E(w, t)$  (dimensions per unit time) to depend on body mass  $w$ :

$$\frac{\partial}{\partial t} E(w, t) = kE(w, t) (p(w)q(w)w^2n(w, t) - c(w)), \quad (4)$$

131 where  $q \leq 1$  is the catchability,  $p$  is the market price of fish (dollars per unit mass),  
 132  $c$  is the unit cost of fishing (dollars) and  $k$  is a constant describing how rapidly effort  
 133 responds to changes in economic returns. For generality, we allow the market price  $p(w)$ ,  
 134 catchability  $q(w)$  and unit cost  $c(w)$  to depend on the body mass targeted.

135 The key assumption underlying the model is that the rate of change of the harvesting  
 136 pressure at a given body mass is proportional to the difference between the revenue from  
 137 that body mass,  $p(w)q(w)E(w, t)w^2n(w, t)$ , and the cost  $c(w)E(w, t)$ , both of which have  
 138 dimensions dollars per unit time. This is a model of a situation, such as a gillnet fishery,  
 139 where individual fishers can decide what size of fish to target via their choice of mesh size  
 140 (Kolding et al., 2015). The fishing effort  $E(w, t)$  represents the total amount of time spent  
 141 by fishers targeting fish of body mass  $w$ . If there is profit to be made from targeting fish  
 142 of mass  $w$ , then more fishers will do so, resulting in an increase in  $E(w, t)$ . If targeting  
 143 fish of mass  $w$  results in a loss, then fishers will cease doing so, resulting in a decrease in  
 144  $E(w, t)$ . This describes an open-access regime, where more people join the fishery when  
 145 it is more profitable than alternative forms of economic activity, and vice versa.

146 The reason for the factor of  $w^2$  in the revenue term is an assumption that fishing gear  
 147 typically targets a percentage range of body masses rather than an absolute range. For  
 148 example, suppose a 5 cm gillnet selects fish from 50 to 100 g. The assumption would then  
 149 be that other size gillnets also select for body masses ranging over a factor of 2 (e.g. 500  
 150 to 1000 g) rather than over a 50 g range. This is consistent with log-normal selectivity  
 151 curves fitted to empirical catch data (Millar and Holst, 1997; Kolding et al., 2015). We  
 152 do not explicitly model individual gears, but this example illustrates the assumption that  
 153 translates into the revenue function seen in Eq. (4) (see Supplementary Material, section  
 154 2 for derivation).

155 Cost in this model includes both actual costs, such as fuel and equipment, and oppor-  
 156 tunity costs. The so-called bioeconomic equilibrium is reached when net profit is zero,  
 157 i.e. when the return from fishing is the same as could be achieved from switching to some  
 158 other form of economic activity. From Eq. (4) we see that the bioeconomic equilibrium  
 159 requires that, for every body mass  $w$ , either  $E(w) = 0$ , or the term in the parentheses is  
 160 zero so that

$$n(w)w^2 = \frac{1}{f(w)q(w)}, \quad (5)$$

161 where  $f(w) = p(w)/c(w)$  is the ratio of unit price to unit cost for fish of body mass  $w$ ,  
 162 which will be referred to as the profitability. Here,  $B(w) = n(w)w^2$  has dimensions of mass  
 163 and represents the amount of biomass in a logarithmic interval at body mass  $w$  in a given  
 164 volume (Andersen and Beyer, 2006). Eq. (5) therefore defines a threshold biomass at  
 165 which targeting fish of a given body mass  $w$  becomes economic. In the exploited size range  
 166 (i.e. body masses for which  $E(w) > 0$ ), the biomass  $B(w)$  must equal the threshold value  
 167 of  $1/(f(w)q(w))$ . In any size range where the biomass  $B(w)$  is less than this threshold,

168 there is no fishing (i.e.  $E(w) = 0$ ). The bioeconomic equilibrium is equivalent to the Nash  
 169 equilibrium in the model of Plank et al. (2016), where a population of fishers  $i = 1, \dots, m$ ,  
 170 each targeting body mass  $w_i$  with fixed fishing capacity, all obtain the same net profit.  
 171 This is also analogous to the “perfect selectivity” results of Diekert (2012), who referred  
 172 to the quantity  $p(w)B(w)$  as the biovalue, and the result that equilibrium net profit is  
 173 zero as dissipation of resource rent.

174 If unit cost, unit price and catchability are all independent of target body mass, then  
 175 Eq. (5) means that biomass  $B(w)$  is constant in the exploited body mass range. This  
 176 corresponds to “invariance of biomass” (*sensu* Sheldon et al., 1977; Boudreau and Dickie,  
 177 1992). The mechanism behind is that, if there are body mass ranges with higher biomass,  
 178 fishers can obtain higher profits by targeting them, which reduces the biomass in until it  
 179 is in line with other body masses (Plank et al., 2016). This means that, once the system  
 180 reaches equilibrium, all fishers obtain the same the catch per unit effort, regardless of the  
 181 body mass they choose to target.

### 182 2.3 Stock-recruitment relationship

183 We examine three different stock-recruitment relationships: (i) constant recruitment; (ii)  
 184 the Beverton and Holt (1957) model; (iii) the Ricker (1954) model. Typically in fisheries,  
 185 recruitment means survival to a certain age, size or life stage. However, for any given  
 186 recruitment size, a fixed proportion of eggs will be recruited under the natural mortality  
 187 model (Andersen and Beyer, 2015). We therefore specify recruitment by specifying the  
 188 rate of production of newborn fish of body mass  $w_0$ , and set  $w_0$  to represent the mass  
 189 of a typical fish egg. As we are dealing with equilibrium solutions, we will omit the  
 190  $t$  argument in the following. The recruitment rate provides a boundary condition for  
 191 the size-structured population model by specifying  $n(w_0)$ , the density of fish of mass  
 192  $w_0$ . Spawning stock biomass  $S$  is calculated as the total biomass of fish greater than a  
 193 specified mass-at-maturation  $w_m$ .

194 Under constant recruitment,  $R = R^*$ , recruitment is entirely decoupled from the  
 195 spawning stock biomass, and hence from the effects of fishing. This is equivalent to a  
 196 yield-per-recruit framework. It also helps isolate the effects of impaired recruitment that  
 197 can arise in the Beverton-Holt and Ricker models.

198 The Beverton-Holt equation for recruitment is an increasing function of  $S$  that satu-  
 199 rates to a maximum recruitment level  $R_{\max}$ :

$$R = R_{\max} \frac{S}{S + S_{50}}, \quad (6)$$

200 where  $S_{50}$  is the spawning stock biomass at which recruitment is at 50% of its maximum.  
 201 To ensure the different stock-recruitment models are comparable, we require that all three

202 models produce the same level of recruitment  $R^*$  when the spawning stock biomass is at  
 203 its unexploited level, which we denote  $S = S^*$ . This condition determines the value of  
 204  $S_{50}$  to be  $S_{50} = S^*(R_{\max}/R^* - 1)$ .

205 Under the Ricker model, recruitment is an increasing function of  $S$  when  $S$  is low,  
 206 but then peaks and starts to decline at higher levels of  $S$ :

$$R = \alpha S e^{-S/\beta}. \quad (7)$$

207 Applying the condition that recruitment must equal  $R^*$  when  $S = S^*$  gives  $\alpha = R^*/S^* e^{S^*/\beta}$ .  
 208 The value of  $\beta$  is then chosen so that the maximum recruitment is  $R_{\max}$  and the unex-  
 209 ploited state is on the declining part of the Ricker curve.

## 210 3 Results

### 211 3.1 Equilibrium solution

212 We begin by presenting an analytical equilibrium solution of the coupled McKendrick-von  
 213 Foerster and Gordon-Schaefer model. Details of the derivation and method for finding  
 214 the exploited body mass range are given in Supplementary Materials, section 3; here we  
 215 present the key results. Under the bioeconomic equilibrium given by Eq. (5), the fishing  
 216 effort in the exploited body mass range is:

$$E(w) = -\frac{w}{q(w)} \frac{d}{dw} \left( \frac{G(w)}{w} \right) - f(w)G(w) \frac{d}{dw} \left( \frac{1}{q(w)f(w)} \right) + \frac{G(w)/w - \mu(w)}{q(w)}. \quad (8)$$

217 This solution applies for any specified functions for profitability  $f(w)$ , catchability  
 218  $q(w)$ , growth rate  $G(w)$  and natural mortality rate  $\mu(w)$ . An important special case is  
 219 when the profitability and catchability are independent of body mass and the growth and  
 220 mortality functions are given by Eqs. (2) and (3). In this case, the fishing effort in Eq.  
 221 (8) is

$$E(w) = (b+1)K \left( \frac{w}{w_\infty} \right)^{-1/b} - bK - \mu_m \left( \frac{w}{w_\infty} \right)^{-\rho}. \quad (9)$$

222 Ecologically, the value of  $\rho$  is expected to be between 0.2 and 0.33, with some evidence  
 223 for  $\rho = 1/3$  (Lorenzen, 1996, 2000).

224 Of interest is the relationship between fishing effort and production, defined as the  
 225 total rate of new biomass production by all fish of body mass  $w$ ,  $P(w) = wn(w)G(w)$ ,  
 226 with dimensions of mass per unit time (note this was termed productivity by Law et al.,  
 227 2016; Plank et al., 2016). In the exploited body mass range, the biomass is constant at

Table 1: Model parameter values.

Parameter	Symbol	Value
von Bertalanffy growth rate	$K$	$0.2 \text{ yr}^{-1}$
Length-weight exponent	$b$	3
Egg mass	$w_0$	0.001 g
Maturation mass	$w_m$	590 g
Asymptotic mass	$w_\infty$	2000 g
Adult natural mortality	$\mu_m$	$0.3 \text{ yr}^{-1}$
Natural mortality exponent	$\rho$	0.2
Maximum recruitment relative to un-exploited state	$R_{\max}/R^*$	1.1

228  $1/f$ , so the production is

$$P(w) = \frac{G(w)}{fw} = \frac{1}{f} \left( bK \left( \frac{w}{w_\infty} \right)^{-1/b} - bK \right). \quad (10)$$

229 Since  $b \approx 3$  and  $\rho$  is close to 0.33, the terms  $(w/w_\infty)^{-1/b}$  and  $(w/w_\infty)^{-\rho}$  in Eqs. (9)  
 230 and (10) are close to being proportional. For values of  $w \ll w_\infty$ , the constant term  
 231  $-bK$  is small relative to the terms of  $w$  and therefore  $E(w)$  and  $P(w)$  will both be almost  
 232 proportional to  $w^{-1/3}$ . As  $w$  gets closer to  $w_\infty$ , the constant term becomes more important  
 233 and so the proportionality between fishing effort and proportionality will become weaker  
 234 close to the asymptotic body mass. This prediction will be tested numerically in the  
 235 following section.

### 236 3.2 Numerical results

237 To calculate explicit equilibrium solutions, numerical values for model parameters are  
 238 needed; these are shown in Table 1. Empirical (McGurk, 1986; Lorenzen, 1996, 2000;  
 239 Gislason et al., 2010) and theoretical (Peterson and Wroblewski, 1984; Andersen and  
 240 Beyer, 2006, 2015; Law et al., 2015) evidence points towards an allometric mortality rate  
 241 with an exponent  $\rho$  in the range 0.2 to 0.33, and we use a value of  $\rho = 0.2$ . We set the  
 242 adult natural mortality rate  $\mu_m$  to be  $1.5K$ , which is one of the Beverton-Holt life-history  
 243 invariants (Charnov and Berrigan, 1991; Jensen, 1996), and is consistent with empirical  
 244 data in many species (Prince et al., 2015; Froese et al., 2016). We study a species with an  
 245 asymptotic body mass of  $w_\infty = 2000$  g and a body mass at maturation of  $w_m = 0.295w_\infty$ ,  
 246 which is consistent with the Beverton-Holt life-history invariant (Charnov and Berrigan,  
 247 1991; Andersen and Beyer, 2015).

248 We first investigate the special case when neither catchability  $q = 1$  nor profitability  
 249  $f = p/c$  vary systematically with body mass. As with the classical Gordon-Schaefer  
 250 model, the profitability (ratio of unit price to unit cost) effectively determines the overall



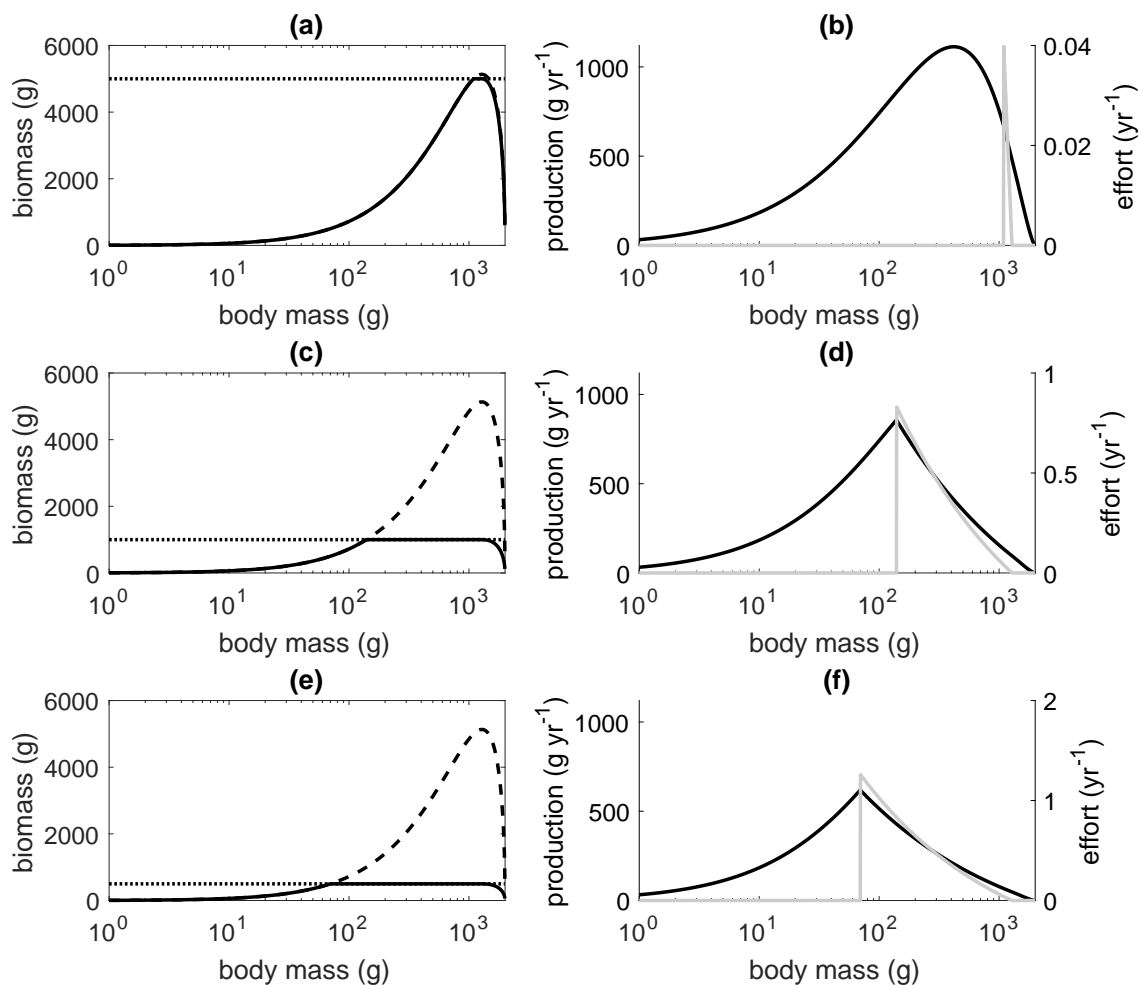


Figure 1: Equilibrium biomass, production and fishing effort against body mass for three levels of profitability  $f$ : (a,b)  $f = 0.2 \times 10^{-3} \text{ g}^{-1}$ ; (c,d)  $f = 10^{-3} \text{ g}^{-1}$ ; (e,f)  $f = 2 \times 10^{-3} \text{ g}^{-1}$ . Left column shows exploited biomass (solid), unexploited biomass (dashed) and critical biomass level for fishing to be economic ( $1/f$ , dotted). When the biomass reaches the critical level, fishing begins and creates a constant biomass solution in the exploited body mass range. Right column shows fishing effort (grey) and production (black). Results are for constant recruitment.

251 level of fishing pressure, with increasing profitability (either high market prices or low  
252 fishing costs) leading to increased effort and decreased stock biomass. If  $f$  is sufficiently  
253 high, overfishing can occur, meaning that stock is depleted below a level that can provide  
254 MSY, or fish are being caught before realising their growth potential. We therefore test  
255 a range of parameter values for  $f$ , ranging from very low, where equilibrium effort is zero  
256 because fishing is not economic, to very high, where overfishing occurs. We investigate  
257 the pattern of size-selectivity, i.e. the relationship between fishing mortality and body  
258 mass, that emerges from the model.

259 Figure 1 shows the biomass  $B(w)$  of the stock, the fishing effort  $E(w)$  and the pro-  
260 duction  $P(w)$  as functions of body mass  $w$ . Results are shown for three different levels of  
261 profitability  $f$ . Solutions are calculated in the size range  $w > 0.001$  g, but only plotted  
262 for  $w > 1$  g as biomass, production and effort are all very small for  $w < 1$  g. Recall from  
263 Eq. (5) that fishing at body mass  $w$  will only take place if the biomass  $B(w)$  reaches the  
264 threshold level  $1/f$ , which is shown as a horizontal dotted lines in Fig. 1(a,c,e). When the  
265 profitability is only just large enough for fishing to be economically viable (Fig. 1(a,b)),  
266 all of the fishing effort is concentrated on the body mass where the biomass peaks, which  
267 for this set of parameters values is a body mass of just over 1000 g. As profitability in-  
268 creases, overall fishing pressure increases, the biomass becomes depleted to the threshold  
269 level over a range of body masses and it becomes equally attractive to fish anywhere in  
270 this range. For example, in Fig. 1(d), fish are being targeted from approximately 100 g  
271 to 1000 g in body mass; the biomass density is constant at  $1/f = 1000$  g within this body  
272 mass range and less than  $1/f$  outside this range (Fig. 1(c)). At these higher levels of  
273 fishing pressure, the distribution of effort over body mass that emerges in the exploited  
274 range range is closely matched to the production (Fig. 1(d,f)), in agreement with the  
275 theoretical predictions.

276 Results for the Beverton-Holt and Ricker stock-recruitment relationships are given in  
277 Supplementary Material, section 4. The only difference relative to the constant recruit-  
278 ment case is that, for a given level of profitability, the minimum body mass exploited  
279 is slightly higher than under constant recruitment. This is because when recruitment  
280 is impaired as a consequence of fishing, biomass does not reach the threshold level for  
281 fishing to be economic until slightly larger body mass (see Supplementary Figures S1-S3).

282 Figure 2(a,b) show how the aggregate yield and aggregate effort (calculated by in-  
283 tegrating yield and effort respectively over all body masses from  $w_0$  to  $w_\infty$ ) vary as  
284 profitability increases. The aggregate effort can be thought of as a measure of the total  
285 number of boat-hours spent fishing. Under all three stock-recruitment relationships, there  
286 is a maximum in the yield curve at an intermediate level of profitability; if profitability  
287 is too high, the yield starts to drop. In the constant recruitment case, this can only be  
288 a result of growth overfishing, i.e. catching fish before they have reached peak cohort  
289 biomass. Under the Beverton-Holt and Ricker models, the maximum occurs at a lower

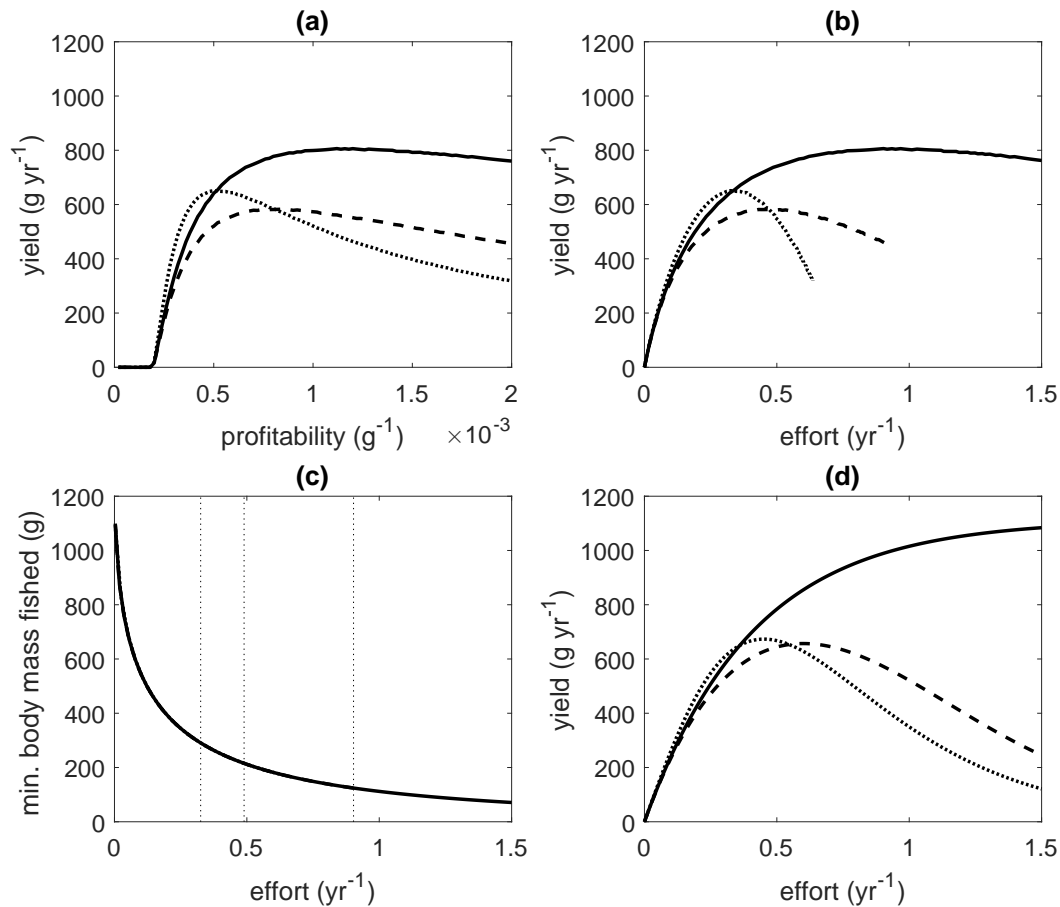


Figure 2: Yield, effort and minimum body mass fished as profitability increases: (a) aggregate yield against profitability  $f$ ; (b) aggregate yield against aggregate effort; (c) minimum body mass fished  $w_{F,\min}$  against aggregate effort; (d) yield against effort for a managed fishery, in which fishing is concentrated at the body mass at which cohort biomass peaks (approx. 420 g). Results are shown for constant (solid), Beverton-Holt (dashed) and Ricker (dotted) stock-recruitment. In (c) the curves are the same for all three stock-recruitment relationships; thin vertical dotted lines indicate the level of fishing effort which maximises yield.

290 levels of profitability and effort and produces a lower yield, than under constant recruit-  
291 ment. This is because recruitment overfishing is possible under the Beverton-Holt and  
292 Ricker models, as well as growth overfishing. Figure 2(c) shows how the smallest body  
293 mass fished  $w_{F,\min}$  changes with increasing effort levels. As effort increases, progressively  
294 smaller fish are caught. For a given level of effort,  $w_{F,\min}$  is independent of the choice of  
295 stock-recruitment relationship.

296 The maximum possible yield in a Beverton-Holt model is achieved when fishing effort  
297 is concentrated on a single size corresponding to the maximum biomass of a cohort  
298 (Beverton and Holt, 1957; Beddington and Kirkwood, 2005; Froese et al., 2016), which  
299 for the parameter values used here occurs at a body mass of approximately 420 g. In  
300 practice, it is impossible to restrict fishing mortality to a single body mass but this  
301 idealised case, sometimes known to as the potential yield (Froese et al., 2016), gives a  
302 useful comparison with the open-access model.

303 Figure 2(d) shows the yield from fishing only at a body mass for 420 g (termed a  
304 managed fishery), as a function of the fishing effort (see Supplementary Material, section  
305 5 for details). For the case of constant recruitment, the yield from the managed fishery  
306 is an increasing function of effort and tends towards the potential yield as the fishing  
307 effort tends to infinity (Beverton and Holt, 1957; Beddington and Kirkwood, 2005). The  
308 potential yield is 38% higher than the maximum yield in the open-access fishery, but  
309 this is an extreme scenario as it corresponds to completely depleting the spawning stock  
310 biomass. For the Beverton-Holt and Ricker recruitment models, the maximum sustainable  
311 yield from the managed fishery is 13% and 3% higher respectively than in the open-access  
312 fishery. As expected, concentrating the fishing mortality at the theoretical optimum body  
313 mass increases yield; however, it is notable that the difference between the maximum  
314 sustainable yields of the managed and open-access fisheries, both of which are idealised  
315 scenarios, is relatively small.

316 We now investigate what happens when there is dependence of profitability (defined as  
317 the ratio of unit price to unit cost) on body mass targeted. We set the profitability  $f(w)$   
318 to be an increasing function of body mass  $w$ . This could model a higher market price  
319 for large fish, a lower cost for targeting large fish, or a combination of both effects. We  
320 choose a function  $f(w)$  for which fish of around 270 g are about half as profitable of fish  
321 of the asymptotic mass of 2000 g (see Supplementary Material, section 5). This makes it  
322 economic to harvest larger fish down to lower biomass. As a result, the threshold biomass  
323 above which fishing is economic is no longer constant, but is a decreasing function of body  
324 mass (Fig. 3(a,c,e)). This shifts the fishing effort towards larger body masses compared  
325 to the results in Fig. 1. Nevertheless, there is still a close correspondence between the  
326 production and the emergent distribution of fishing effort over body mass in Fig. 3(d,f).  
327 We also tested the effect of setting the catchability  $q(w)$  to be an increasing function of  
328 body mass  $w$ . This models a situation where large fish are easier to catch than small

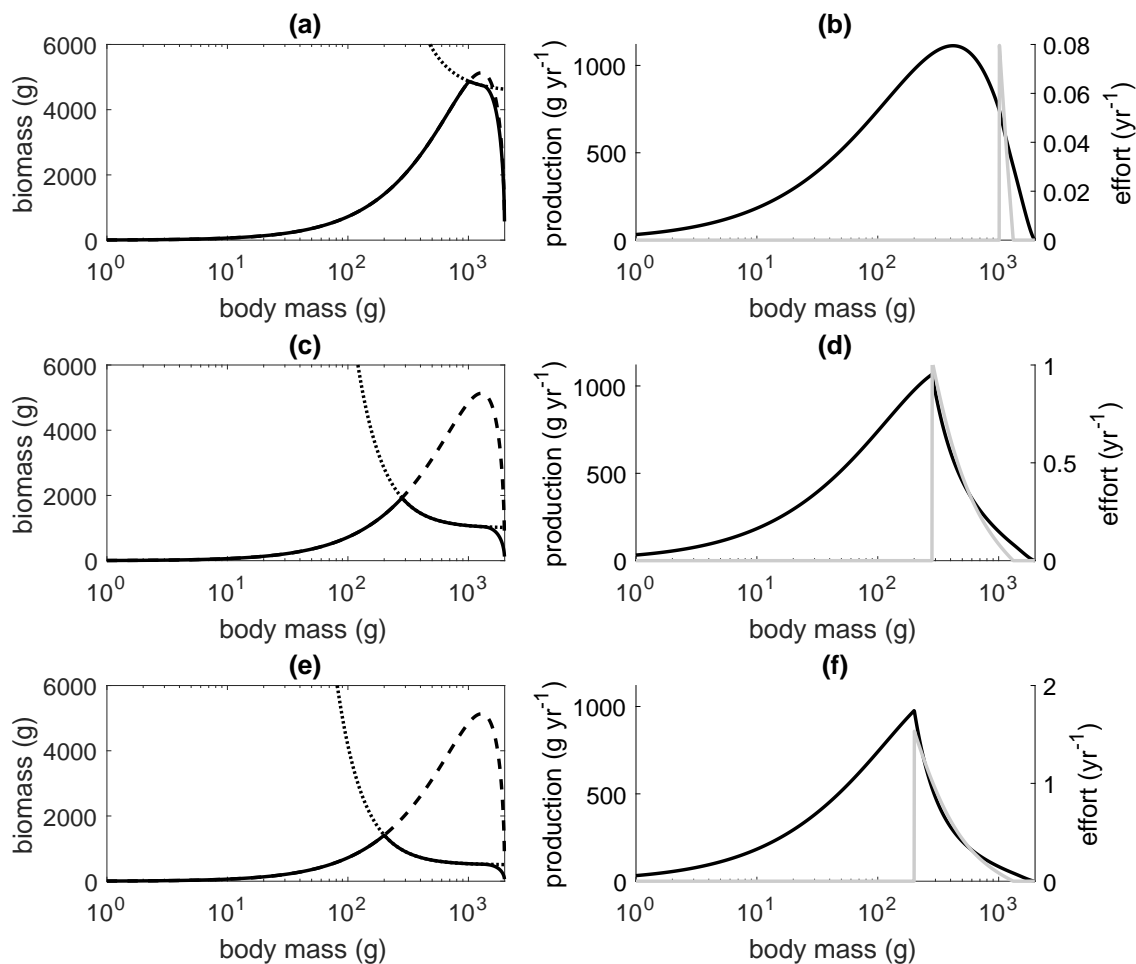


Figure 3: Equilibrium biomass, production and fishing effort against body mass where large fish fetch a higher unit price than small fish, and three levels of maximum profitability  $f_{\max}$ : (a,b)  $f_{\max} = 0.2 \times 10^{-3} \text{ g}^{-1}$ ; (c,d)  $f_{\max} = 0.6 \times 10^{-3} \text{ g}^{-1}$ ; (e,f)  $f_{\max} = 2 \times 10^{-3} \text{ g}^{-1}$ . Left column shows exploited biomass (solid), unexploited biomass (dashed) and critical biomass level for fishing to be economic ( $1/f(w)$ , dotted). Right column shows fishing effort (grey) and production (black). Results are for constant recruitment.

329 ones for the same amount of time spent fishing. This could be because schools of larger  
330 fish are easier to locate using sonar equipment, or because the gear used to catch larger  
331 fish is more efficient. This results in the same fishing mortality as in Fig. 3, but higher  
332 fishing effort is required at smaller body masses within the targeted range to compensate  
333 for the reduced catchability (see Supplementary Fig. S5).

## 334 4 Discussion

335 We have investigated a size-structured bioeconomic model which allows fishing effort to  
336 vary as a function of body mass. The effort at a given body mass will increase if fishing  
337 that body mass returns a positive net profit (i.e. revenue from catch per unit effort  
338 exceeds cost per unit effort) and will decrease if it returns a net loss. This is an extension  
339 of the Gordon-Schaefer model (Gordon, 1954; Schaefer, 1954) to allow fishing effort to  
340 depend on body mass. The model assumes that the market price of fish is independent of  
341 the size of the catch. In reality, price will depend on supply and this could be modelled  
342 by an elasticity relationship.

343 The result that an open-access fishery, combined with perfect size selectivity, leads to  
344 net profit from fishing being equalised to zero across body sizes is not new. Diekert (2012)  
345 demonstrated this using a similar model and referred to it as dissipation of rents along the  
346 dimension of size. The new result presented here is that, at equilibrium, the aggregate  
347 fishing mortality is closely matched to production across body sizes. We have tested this  
348 in a model with constant recruitment (equivalent to a yield-per-recruit calculation) and  
349 two different stock-recruitment relationships. When market price, cost and catchability  
350 are independent of body mass, fishing is predicted to lead to a constant distribution of  
351 biomass in logarithmic body mass intervals. We have also tested scenarios in which either  
352 the ratio of unit price to unit cost, or the catchability, is an increasing function of body  
353 mass.

354 The close match between fishing mortality and production across body sizes corre-  
355 sponds to BH within a single species. This is an emergent outcome of the model, rather  
356 than an externally applied rule, providing a counterpoint to arguments that implementa-  
357 tion of BH would require impractical levels of monitoring, micromanagement and enforce-  
358 ment (Burgess et al., 2015; Froese et al., 2015; Reid et al., 2016). It also confirms that  
359 this outcome is not limited to size-spectrum models (Plank et al., 2016) and is robust to  
360 model selection. Interestingly, the match between fishing mortality and production only  
361 applies for body sizes down to a minimum capture size, below which fishing is not eco-  
362 nomically attractive. This suggests a more nuanced definition of BH across body sizes as:  
363 “a moderate mortality from fishing applied to sizes above the size at which production is  
364 maximal, and distributed in proportion to production”. However, the most appropriate  
365 definition depends on the relative values placed on competing objectives, such as yield,

366 profit and conservation, and the consequences of this alternative definition require further  
367 research. In addition, it is important to recognise that the size at which production peaks  
368 (or equivalently cohort biomass peaks Law et al., 2016), although classically treated as a  
369 fixed externality, in reality will vary as a consequence of fishing changing the growth and  
370 mortality rates at different sizes (Plank et al., 2016).

371 Our argument is not about fishing patterns or management strategies that maximise  
372 either yield or profit. Instead, they are a prediction about the pattern that would emerge  
373 as a consequence of size-selectivity decisions made by independent fishing agents. The  
374 yield obtained under such a pattern is not the global maximum sustainable yield, which for  
375 the Beverton-Holt model is theoretically obtained by fishing exclusively at  $l_{\text{opt}}$  – the size  
376 at which unexploited cohort biomass is maximal (Beverton and Holt, 1957; Beddington  
377 and Kirkwood, 2005). Nonetheless, the predicted yield from allowing fishing agents to  
378 choose what size fish to target is only slightly lower than the theoretical maximum. This  
379 is a counterpoint to the results of Froese et al. (2016), which showed that, if fishing  
380 mortality is constant above size at first capture, then targeting small fish significantly  
381 reduces yield (growth overfishing). This does not happen in our bioeconomic model  
382 because fishing mortality is not constrained to be the same at all body sizes, but is  
383 allowed to adapt to the net profit obtained by targeting different sizes. Production is a  
384 decreasing function of body mass for sufficiently large fish and, when size-selectivity is  
385 the product of the actions of independent fishing agents, the aggregate fishing mortality  
386 reflects this declining production at large sizes.

387 If the objective is to maximise the profit of a fishing monopolist, the theoretical  
388 solution is to fish exclusively at the size at which biovalue is maximised (which may be  
389 greater than  $l_{\text{opt}}$  if larger fish have higher value unit value) at a fishing mortality less  
390 than  $F_{\text{MSY}}$  (Diekert, 2012). As with the classical Gordon-Schaefer model, net profit at  
391 the bioeconomic equilibrium is zero by definition. This means that the economic return  
392 from fishing, over a range of body sizes, is the same as could be obtained from alternative  
393 economic activity. This is the predicted outcome of an open-access regime, where agents  
394 can enter the fishery as long as it is profitable to do so. If the cost of fishing is low (or the  
395 economic prospects from alternative activities are poor), this leads to depletion of the  
396 stock below the level that can provide MSY. This is a well-known property of open-access  
397 models (Schaefer, 1954), rather than of the distribution of fishing effort over body sizes  
398 *per se*. We are not advocating open-access fishing: controls on fishing effort are clearly  
399 needed to prevent overfishing, irrespective of the pattern of size selectivity.

400 The predicted match between fishing effort a production has been observed in small-  
401 scale African freshwater fisheries, for example Lake Kariba between Zambia and Zim-  
402 babwe (Kolding et al., 2015), the Bangweulu Swamps in Northern Zambia (Kolding et al.,  
403 2003) and Lake Volta in Ghana (Kolding and van Zwieten, 2014). In these examples, ag-  
404 gregate fishing mortality is the product of a large number of individual fishers employing

405 a wide range of gear types and mesh sizes, often without effective size-based regulations  
406 (Kolding and van Zwieten, 2011; Mills et al., 2011). The pattern of size-selectivity in  
407 large-scale, commercial fisheries is clearly very different. This is a consequence partly  
408 of size-based regulations prohibiting the targeting of small fish, and partly of the size-  
409 selectivity of the fishing gears in use. Trawl fishing typically selects all fish larger than a  
410 certain size and the current model is not equipped to describe this situation. The model  
411 could be modified to investigate trawl fisheries, for example by making the aggregate  
412 fishing mortality the sum of a set of S-shaped or knife-edge selectivity curves. Diekert  
413 (2012) showed that this resulted in a similar trend towards catching fish smaller than  $l_{\text{opt}}$   
414 and decreasing resource rents, but the relation between the emergent pattern of fishing  
415 mortality and production deserves further investigation.

416 It has been argued that the requirement of BH to fish is proportion to production  
417 would require infeasible levels of monitoring of production and micromanagement of fish-  
418 ing effort (Burgess et al., 2015; Froese et al., 2015; Reid et al., 2016). Our results show  
419 that a balanced distribution of fishing effort across body mass can emerge, at least approx-  
420 imately, from the behaviour of independent agents trying to maximise their own economic  
421 returns. In reality, size selectivity is the product of numerous factors, including gear type,  
422 mesh size, species morphology and behaviour, and spatiotemporal deployment of fishing  
423 effort. Many of these factors are difficult to control and it is unlikely we will ever be able  
424 to target fish with perfect selectivity (Breen et al., 2016). Our results should not be seen  
425 as quantitatively realistic predictions, but they do reveal an underlying, self-organising  
426 principle by which fishing effort becomes matched with production.

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## 431 References

- 432 Andersen, K. H. and Beyer, J. E. (2006). Asymptotic size determines species abundance  
433 in the marine size spectrum. *The American Naturalist*, 168(1):54–61.
- 434 Andersen, K. H. and Beyer, J. E. (2015). Size structure, not metabolic scaling rules,  
435 determines fisheries reference points. *Fish and Fisheries*, 16(1):1–22.
- 436 Andersen, K. H., Blanchard, J. L., Fulton, E. A., Gislason, H., Jacobsen, N. S., and  
437 van Kooten, T. (2016). Assumptions behind size-based ecosystem models are realistic.  
438 *ICES Journal of Marine Science*, fsv211.



- 439 Beddington, J. R. and Kirkwood, G. P. (2005). The estimation of potential yield and  
440 stock status using life–history parameters. *Philosophical Transactions of the Royal*  
441 *Society of London B: Biological Sciences*, 360(1453):163–170.
- 442 Benoît, E. and Rochet, M.-J. (2004). A continuous model of biomass size spectra gov-  
443 erned by predation and the effects of fishing on them. *Journal of Theoretical Biology*,  
444 226(1):9–21.
- 445 Beverton, R. J. H. and Holt, S. J. (1957). *On the Dynamics of Exploited Fish Populations*.  
446 Springer.
- 447 Boudreau, P. R. and Dickie, L. M. (1992). Biomass spectra of aquatic ecosystems in rela-  
448 tion to fisheries yield. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(8):1528–  
449 1538.
- 450 Breen, M., Graham, N., Pol, M., He, P., Reid, D., and Suuronen, P. (2016). Selective  
451 fishing and balanced harvesting. *Fisheries Research*.
- 452 Burgess, M. G. (2015). Consequences of fleet diversification in managed and unmanaged  
453 fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(1):54–70.
- 454 Burgess, M. G., Diekert, F. K., Jacobsen, N. S., Andersen, K. H., and Gaines, S. D.  
455 (2015). Remaining questions in the case for balanced harvesting. *Fish and Fisheries*,  
456 doi:10.1111/faf.12123.
- 457 Charnov, E. L. and Berrigan, D. (1991). Evolution of life history parameters in animals  
458 with indeterminate growth, particularly fish. *Evolutionary Ecology*, 5(1):63–68.
- 459 Christensen, V. and Pauly, D. (1992). ECOPATH II - a software for balancing steady-  
460 state ecosystem models and calculating network characteristics. *Ecological Modelling*,  
461 61(3):169–185.
- 462 Diekert, F. K. (2012). Growth overfishing: the race to fish extends to the dimension of  
463 size. *Environmental and Resource Economics*, 52(4):549–572.
- 464 Froese, R., Walters, C., Pauly, D., Winker, H., Weyl, O. L. F., Demirel, N., Tsikliras,  
465 A. C., and Holt, S. J. (2015). A critique of the balanced harvesting approach to fishing.  
466 *ICES Journal of Marine Science*, fsv122.
- 467 Froese, R., Winker, H., Gascuel, D., Sumalia, U. R., and Pauly, D. (2016). Minimizing  
468 the impact of fishing. *Fish and Fisheries*, doi:10.1111/faf.12146.
- 469 Garcia, S., Rice, J., and Charles, A. (2015). Balanced harvesting in fisheries: a prelimi-  
470 nary analysis of management implications. *ICES Journal of Marine Science*, fsv156.

- 471 Garcia, S. M., Kolding, J., Rice, J., Rochet, M.-J., Zhou, S., Arimoto, T., Beyer, J. E.,  
472 Borges, L., Bundy, A., Dunn, D., Fulton, E. A., Hall, M., Heino, M., Law, R., Makino,  
473 M., Rijnsdrop, A. D., Simard, F., and Smith, A. D. M. (2012). Reconsidering the  
474 consequences of selective fisheries. *Science*, 335(6072):1045–1047.
- 475 Gillis, D. M., Peterman, R. M., and Tyler, A. V. (1993). Movement dynamics in a fishery:  
476 application of the ideal free distribution to spatial allocation of effort. *Canadian Journal*  
477 *of Fisheries and Aquatic Sciences*, 50(2):323–333.
- 478 Gillis, D. M. and van der Lee, A. (2012). Advancing the application of the ideal free  
479 distribution to spatial models of fishing effort: the isodar approach. *Canadian Journal*  
480 *of Fisheries and Aquatic Sciences*, 69(10):1610–1620.
- 481 Gislason, H., Daan, N., Rice, J. C., and Pope, J. G. (2010). Size, growth, temperature  
482 and the natural mortality of marine fish. *Fish and Fisheries*, 11(2):149–158.
- 483 Gordon, H. S. (1954). The economic theory of a common-property resource: the fishery.  
484 *Journal of Political Economy*, 62:124–142.
- 485 Hixon, M. A., Johnson, D. W., and Sogard, S. M. (2014). BOFFFFs: on the importance  
486 of conserving old-growth age structure in fishery populations. *ICES Journal of Marine*  
487 *Science*, 71(8):2171–2185.
- 488 Hsieh, C.-h., Yamauchi, A., Nakazawa, T., and Wang, W.-F. (2010). Fishing effects on  
489 age and spatial structures undermine population stability of fishes. *Aquatic Sciences*,  
490 72(2):165–178.
- 491 Jensen, A. L. (1996). Beverton and Holt life history invariants result from optimal trade-  
492 off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences*,  
493 53(4):820–822.
- 494 Kolding, J., Jacobsen, N. S., Andersen, K. H., van Zwieten, P. A. M., and Giacomini, H.  
495 (2015). Maximizing fisheries yields while maintaining community structure. *Canadian*  
496 *Journal of Fisheries and Aquatic Sciences*, 73(999):1–12.
- 497 Kolding, J., Ticheler, H., and Chanda, B. (2003). The Bangweulu swamps – a balanced  
498 small-scale multi-species fishery. In *Management, co-management or no management?*  
499 *Major dilemmas in southern African freshwater fisheries. Part 2: case studies. FAO*  
500 *Fisheries Technical Paper 426/2*, pages 34–66. FAO, Rome.
- 501 Kolding, J. and van Zwieten, P. A. M. (2011). The tragedy of our legacy: how do  
502 global management discourses affect small scale fisheries in the south? In *Forum for*  
503 *Development Studies*, volume 38, pages 267–297. Taylor & Francis.

- 504 Kolding, J. and van Zwieten, P. A. M. (2014). Sustainable fishing of inland waters.  
505 *Journal of Limnology*, 73:128–144.
- 506 Laugen, A. T., Engelhard, G. H., Whitlock, R., Arlinghaus, R., Dankel, D. J., Dunlop,  
507 E. S., Eikeset, A. M., Enberg, K., Jørgensen, C., Matsumura, S., et al. (2014). Evolu-  
508 tionary impact assessment: accounting for evolutionary consequences of fishing in an  
509 ecosystem approach to fisheries management. *Fish and Fisheries*, 15(1):65–96.
- 510 Law, R., Kolding, J., and Plank, M. J. (2015). Squaring the circle: reconciling fishing  
511 and conservation of aquatic ecosystems. *Fish and Fisheries*, 16(1):160–174.
- 512 Law, R., Plank, M. J., and Kolding, J. (2012). On balanced exploitation of marine ecosys-  
513 tems: results from dynamic size spectra. *ICES Journal of Marine Science*, 69(4):602–  
514 614.
- 515 Law, R., Plank, M. J., and Kolding, J. (2016). Balanced exploitation and coexistence of  
516 interacting, size-structured, fish species. *Fish and Fisheries*, 17:281–302.
- 517 Lorenzen, K. (1996). The relationship between body weight and natural mortality in  
518 juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal*  
519 *of Fish Biology*, 49(4):627–642.
- 520 Lorenzen, K. (2000). Allometry of natural mortality as a basis for assessing optimal  
521 release size in fish-stocking programmes. *Canadian Journal of Fisheries and Aquatic*  
522 *Sciences*, 57(12):2374–2381.
- 523 McGurk, M. D. (1986). Natural mortality of marine pelagic fish eggs and larvae: role of  
524 spatial patchiness. *Marine Ecology Progress Series*, 34(3):227–242.
- 525 McKendrick, A. G. (1925). Applications of mathematics to medical problems. *Proceedings*  
526 *of the Edinburgh Mathematical Society*, 44:98–130.
- 527 Millar, R. B. (1992). Estimating the size-selectivity of fishing gear by conditioning on  
528 the total catch. *Journal of the American Statistical Association*, 87(420):962–968.
- 529 Millar, R. B. and Holst, R. (1997). Estimation of gillnet and hook selectivity using  
530 log-linear models. *ICES Journal of Marine Science*, 54(3):471–477.
- 531 Mills, D. J., Westlund, L., de Graaf, G., Kura, Y., Willman, R., and Kelleher, K. (2011).  
532 Under-reported and undervalued: small-scale fisheries in the developing world. In  
533 *Small-scale fisheries management: frameworks and approaches for the developing world*,  
534 pages 1–15. CAB International, United Kingdom.
- 535 Peterson, I. and Wroblewski, J. S. (1984). Mortality rate of fishes in the pelagic ecosystem.  
536 *Canadian Journal of Fisheries and Aquatic Sciences*, 41(7):1117–1120.

- 537 Plank, M. J., Kolding, J., Law, R., Gerritsen, H. D., and Reid, D. (2016). Balanced  
538 harvesting can emerge from fishing decisions by individual fishers. *Fish and Fisheries*,  
539 doi:10.1111/faf.12172.
- 540 Prince, J., Hordyk, A., Valencia, S. R., Loneragan, N., and Sainsbury, K. (2015). Re-  
541 visiting the concept of Beverton–Holt life-history invariants with the aim of informing  
542 data-poor fisheries assessment. *ICES Journal of Marine Science*, 72(1):194–203.
- 543 Quaas, M. F., Requate, T., Ruckes, K., Skonhott, A., Vestergaard, N., and Voss, R.  
544 (2013). Incentives for optimal management of age-structured fish populations. *Resource*  
545 *and Energy Economics*, 35(2):113–134.
- 546 Ravn-Jonsen, L. J. (2011). Intertemporal choice of marine ecosystem exploitation. *Eco-  
547 logical Economics*, 70(10):1726–1734.
- 548 Reid, D. G., Graham, N., Suuronen, P., He, P., and Pol, M. (2016). Implementing  
549 balanced harvesting: practical challenges and other implications. *ICES Journal of  
550 Marine Science*, fsv253.
- 551 Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board  
552 of Canada*, 11(5):559–623.
- 553 Schaefer, M. B. (1954). Some aspects of the dynamics of populations important to  
554 the management of the commercial marine fisheries. *Inter-American Tropical Tuna  
555 Commission Bulletin*, 1(2):27–56.
- 556 Sheldon, R. W., Sutcliffe Jr, W. H., and Paranjape, M. A. (1977). Structure of pelagic  
557 food chain and relationship between plankton and fish production. *Journal of the  
558 Fisheries Research Board of Canada*, 34(12):2344–2353.
- 559 Sparre, P. and Venema, S. C. (1989). *Introduction to tropical fish assessment. Part I:  
560 Manual*. FAO, Rome.
- 561 Tahvonen, O. (2009). Economics of harvesting age-structured fish populations. *Journal  
562 of Environmental Economics and Management*, 58(3):281–299.
- 563 van Putten, I. E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K. G., Hutton, T.,  
564 and Pascoe, S. (2012). Theories and behavioural drivers underlying fleet dynamics  
565 models. *Fish and Fisheries*, 13(2):216–235.
- 566 von Bertalanffy, L. (1957). Quantitative laws in metabolism and growth. *Quarterly  
567 Review of Biology*, 32:217–231.

568 von Foerster, H. (1959). Some remarks on changing populations. In Stohlman, F. J.,  
569 editor, *The Kinetics of Cellular Proliferation*, pages 382–407. Grune and Stratton,  
570 New York.