UNIVERSITY of York

This is a repository copy of Balanced harvesting could reduce fisheries-induced evolution.

White Rose Research Online URL for this paper: <u>https://eprints.whiterose.ac.uk/137827/</u>

Version: Accepted Version

Article:

Law, Richard orcid.org/0000-0002-5550-3567 and Plank, Michael (2018) Balanced harvesting could reduce fisheries-induced evolution. Fish and fisheries. pp. 1078-1091. ISSN 1467-2960

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk https://eprints.whiterose.ac.uk/

Balanced harvesting could reduce fisheries-induced evolution

Richard Law, Michael J. Plank

May 31, 2018

Alternative title: On fisheries-induced evolution under balanced harvesting Running title: Selection and balanced harvesting

Richard Law: York Cross-Disciplinary Centre for Systems Analysis, Ron Cooke Hub, University of York, York YO10 5GE, UK

Michael J. Plank: School of Mathematics and Statistics and Te Pūnaha Matatini, University of Canterbury, Christchurch, New Zealand

Abstract

Current fisheries management pays little attention to fisheriesinduced evolution. Methods of exploitation that have benefits in the short term, while ameliorating selection in the longer term would therefore be advantageous. Balanced harvesting (BH) is a potential candidate. This tries to bring fishing more in line with natural production, and some short-term benefits for conservation of aquatic ecosystems and for biomass yield have already been documented. It is also predicted to be relatively benign as a selective force on fish stocks, because it keeps the overall distribution of mortality relatively close to natural mortality.

We test this prediction, coupling an ecological model of marine, size-spectrum dynamics to an adaptive-dynamics model of lifehistory evolution. The evolutionary variable is the reproductive schedule, set by the maximum body mass and the mass at maturation. The prediction is supported by our numerical analysis: directional selection under BH is approximately an order of magnitude weaker than in a standard fishery in which fish experience a fixed rate of fishing mortality after recruitment. The benefit of BH follows from relatively little fishing on large fish, due to the low somatic production rates these big fish have. These results therefore support the general argument for protecting big, old fish, both for ecological and for evolutionary reasons. Slot fisheries that protect large fish share some qualitative features with BH, and show similar evolutionary benefits.

Keywords: adaptive dynamics, ecosystem dynamics, fishing-induced selection, life-history evolution, production rate, size spectrum

Contents

- 1. Introduction
- 2. Theory
 - 2.1 Ecological model
 - 2.2 Evolutionary model
 - 2.3 Strength of directional selection from fishing
- 3. Numerical results
 - 3.1 Ancestral singular point of evolution
 - 3.2 Patterns of fishing mortality
 - 3.3 Mortality from mackerel predation
 - 3.4 Selection in BH and SAE fisheries
 - 3.5 Selection in slot fisheries
- 4. Discussion
- 5. Acknowledgements

1 **Introduction**

Fisheries are potentially important drivers of evolution in fish stocks, because fishing is often a major cause of mortality once fish reach a size at 3 which they are harvested (Heino et al., 2015). There is good evidence 4 for phenotypic change in wild populations consistent with expected effects 5 of fishing, including the much-discussed case of maturation in North East 6 Arctic cod (Eikeset et al., 2016; Enberg and Jørgensen, 2017). There is also experimental evidence that such evolution can take place (Haugen 8 and Vøllestad, 2001; Conover and Munch, 2002; van Wijk et al., 2013). 9 A molecular-genetic basis for such evolution, built on change in gene fre-10 quencies at loci linked to traits under selection in the wild, is also being 11 developed (e.g. Chebib et al., 2016). 12

The precautionary principle calls for the minimization of risks from 13 fisheries-induced evolution (FIE). We are the custodians of marine ecosys-14 tems, and responsible for leaving them undamaged for the future. This is 15 enshrined in the Malawi Principle 5 of the Convention on Biological Diver-16 sity that motivates the ecosystem-based approach to fisheries management. 17 However, despite the case for evolutionary impact assessment (Jørgensen 18 et al., 2007), the day-to-day reality is that short-term issues of manage-19 ment supercede longer-term issues of FIE (Law, 2007). An example is the 20 plan of the European Union to eliminate discarding of species subject to 21 quota or minimum landing-size regulations in European waters (Common 22 Fisheries Policy reform EU Regulation 1380/2013). This is leading to the 23 development of technical measures that will increase the selectivity of fish-24 ing, without consideration of the longer-term consequences for FIE. The 25 short-term solution comes potentially at the cost of exacerbating another, 26 longer-term problem. 27

One way forward would be to develop methods of fishing that help in 28 the immediate future and, at the same time, ameliorate selection in the 29 longer term (Law, 2007). Balanced harvesting (BH) is a potential candidate 30 for this. BH has been proposed as a way of exploiting fish stocks that 31 would help to maintain the structure and functioning of marine ecosystems, 32 by bringing fishing mortality more in line with the natural production of 33 biomass by species and body sizes (Garcia et al., 2012). For clarity, we 34 define BH at the outset as setting fishing mortality rate to be proportional 35 to the rate of somatic production (dimensions: mass vol. $^{-1}$ time $^{-1}$, or mass 36 $\operatorname{area}^{-1} \operatorname{time}^{-1}$). Perfect BH of an ecosystem is probably unachievable, but 37 it does suggest a direction to go in. The bar for improvement appears to 38 be low: no relationship could be found between fishing mortality rate and 39 production rate of species in a recent study on the West of Scotland shelf 40 ecosystem (Heath et al., 2017). Matters could be improved both by a better 41

balance of fishing mortality across species, and also by a better balance 42 across body sizes within species. These paths towards a better balance are 43 complementary, and both could bring fishing more in line with production 44 rates. Both are the subject of research, including the distribution of fishing 45 among species or functional groups (Garcia et al., 2012; Kolding et al., 46 2016a; Heath et al., 2017), and the distribution of fishing over body sizes 47 (Law et al., 2012; Jacobsen et al., 2014; Kolding et al., 2016b; Law et al., 48 2016). 49

Several short-term benefits of BH have been documented. The open-50 access fisheries on the Zambian side of Lake Kariba, with patterns of fishing 51 mortality closer to BH than the more regulated fisheries of Zimbabwe, give 52 greater biomass yields with less impact on community structure (Kolding 53 et al., 2016b). Reducing fishing mortality in species with low production 54 rate helps to protect those that are rare and vulnerable (Law et al., 2016). 55 It also reduces 'longevity overfishing', aiding the recovery of natural size 56 structures, by allowing more survival of large individuals (Beamish et al., 57 2006). In this way, it improves the resilience of stocks to external pertur-58 bations (Hixon et al., 2014). 59

Here we consider a by-product of BH, that could have longer-term ben-60 efits of slowing down FIE. This is motivated by models that suggest BH 61 keeps total mortality within species closer to natural mortality than do 62 traditional size-at-entry (SAE) fisheries (Law et al., 2015, 2016). A better 63 alignment between fishing mortality and natural mortality should reduce 64 selection on the life-histories of fish stocks, and therefore reduce FIE. This 65 is primarily a prediction about the distribution of fishing mortality over 66 body size within species, i.e. about BH across body sizes within species, 67 rather than about BH across species. The purpose of this paper is to test 68 this prediction about BH. Our numerical results support it. In other words, 69 BH has an incidental, longer-term advantage of reducing directional selec-70 tion from fishing, in addition to its short-term benefits on structure and 71 functioning of marine ecosystems. 72

To do this work, we developed a method to connect the ecological dynamics of size spectra to a simple evolutionary model of adaptive dynamics (AD) (Kisdi and Geritz, 2010; Brännström et al., 2013). In technical terms, the work involves analysis of a transversal eigenvalue (the invasion fitness) of a high-dimensional Jacobian. The Jacobian can be resolved to a simple form that will allow broader study of evolution in complex, size-structured, marine ecosystems in the future.

$_{10}$ 2 Theory

The theory is built in three steps (Fig. 1). (Step 1) An ecological model 81 of the dynamics of coupled size spectra: this is needed because there is no 82 external notion of fitness in an AD model—fitness of genetically distinct 83 phenotypes emerges directly from the ecological processes. (Step 2) An 84 evolutionary model based on AD within which the ecological dynamics are 85 nested: this moves an ancestral population through a sequence of muta-86 tion and selection events, driven by predation in the size spectra, leading 87 eventually to a singular point at which there is no further evolution. The 88 system is then at an evolutionarily stable state (ESS), before fishing is 89 added. Without a separation of this kind, selection from fishing would be 90 conflated with selection from predation taking place inside the food web. 91 (Step 3) Calculation of the strength and direction of selection generated by 92 a range of patterns of fishing at the ESS. 93

94 FIGURE 1 NEAR HERE

95 2.1 Ecological model

Dynamic size-spectrum models of marine ecosystems couple together an 96 arbitrary number of species through size-dependent feeding (Andersen and 97 Beyer, 2006; Hartvig et al., 2011; Blanchard et al., 2014; Jacobsen et al., 98 2014). Like any model of a complex, real-world marine ecosystems, they 99 are a simplification. However, they are built up from realistic assumptions 100 about the frequency of predator-prev interactions between individuals of 101 a given size (Andersen et al., 2016). First, they assume that body size 102 is the primary driver of the trophic level at which marine organisms feed. 103 This property of marine trophic structure is in keeping with empirical re-104 search on stable isotopes of nitrogen (Jennings et al., 2001). Second, they 105 deal explicitly with the growth of individuals as they eat other smaller or-106 ganisms, so there is no external growth model, such as a von Bertalanffy 107 growth equation. Third, they assume that the most common cause of death 108 is through being eaten by larger organisms, which leaves less uncertainty 109 about rates of natural mortality. Fourth, they assume that species are 110 coupled through the body-size dependence of their prey: they are both 111 predators on other species, and cannibals on themselves. Different species 112 clearly can specialise in ways that affect their locations in food webs, and 113 size-spectrum models incorporate some species-dependent feeding param-114 eters. Importantly, unlike most models in fisheries science, size-spectrum 115 models do the bookkeeping of biomass flowing in and out of species and 116 size categories, as individuals eat one another and grow (e.g. Law et al., 117

118 2016).

The state variables of size-spectrum models are functions that describe 119 the density of organisms $\phi_i(w,t)$ as functions of body mass w and time t, 120 where i is an index for species. The core of such a model is a system of par-121 tial differential equations (PDEs), one equation for each species, describing 122 how the density function $\phi_i(w,t)$ of each species unfolds over time through 123 feeding (and consequent growth, reproduction and death). At their sim-124 plest, the PDEs take the form of a McKendrick—von Foerster equation, 125 with body mass rather than age being the independent variable (Sinko and 126 Streiffer, 1971; Silvert and Platt, 1978): 127

$$\frac{\partial}{\partial t}\phi_i = \overbrace{-\frac{\partial}{\partial w}\left[\tilde{g}_i\phi_i\right]}^{(a)} - \overbrace{\tilde{\mu}_{\text{tot},i}\phi_i}^{(b)}.$$
(2.1)

128

To help understand this equation, Fig. 2 shows the meaning of terms on the 129 right-hand side. Term (a) describes the change in density at body mass w, 130 due to feeding on smaller fish, contained in the function $\tilde{g}_i(w,t)$ the growth 131 rate of individuals of body mass w at time t. This is calculated as a function 132 of the abundance of smaller, conspecific and heterospecific individuals, of a 133 suitable size to be prev of a individual of body mass w. Term (b) describes 134 the change in density at body mass w, due to death; $\tilde{\mu}_{tot,i}(w,t)$ is the total 135 per capita death rate for individuals of body mass w. This is calculated 136 as a function of the abundance of larger, conspecific and heterospecific 137 individuals of a suitable size to be predators of an individual of body mass 138 w at time t, plus other sources of mortality including senses and fishing. 139 See Appendix A for full mathematical details. 140

141 FIGURE 2 NEAR HERE

In addition to species-dependent feeding, multispecies size spectra allow 142 species to have different life histories. Life-history parameters include, for 143 instance, the asymptotic body mass $w_{i,\infty}$, and body mass at 50 % mat-144 uration $w_{i,m}$. In non-seasonal, size-spectrum models, individuals allocate 145 an increasing proportion of incoming biomass towards reproduction and 146 away from somatic growth as they mature, the proportion reaching 1 at 147 $w_{i,\infty}$ where somatic growth ends. For a given egg size, this is enough to 148 define a schedule of reproduction at the level of species. Predation mor-149 tality and growth, which are also components of the life history, are not 150 set as externalities in size-spectrum models, as they emerge from size- and 151 density-dependent feeding in the food web. However, some additional death 152 is incorporated, recognising that predation is not the only reason why or-153 ganisms die, and such death may include mortality from fishing. In this 154 way the life history is defined at the species level. 155

Note that the smallest organisms must have food to eat if they are to 156 grow, so size spectra have to be extended down into the spectrum of uni-157 cellular plankton. For simplicity, we used a fixed plankton spectrum, set to 158 values that correspond approximately to those observed. This is equivalent 159 to an assumption that the plankton dynamics happen on a faster timescale 160 and cannot be exhausted by predation, and it has the effct that fish popu-161 lation growth is not limited by the plankton. However, the predation and 162 cannibalism among the fish are enough to hold their population growth in 163 check, as long as the upper limit of plankton body size is kept sufficiently 164 small relative to the sizes of maturation in the fish species. 165

¹⁶⁶ 2.2 Evolutionary model

We used adaptive dynamics (AD) to describe phenotypic evolution. AD 167 was developed in the 1990s to provide a direct link between population 168 dynamics and phenotypic evolution (Kisdi and Geritz, 2010). The basic 169 dynamics and their graphical representation were given in some early pa-170 pers (Metz et al., 1992; Dieckmann and Law, 1996; Metz et al., 1996; Geritz 171 et al., 1998), and a review by Brännström et al. (2013) gives an overview 172 of the subject. The idea is that phenotypic traits, such as asymptotic 173 body mass $w_{i,\infty}$, although fixed in ecological time, have a genetic com-174 ponent that is under selection driven directly by the ecological processes. 175 In the context of multispecies size spectra, AD allows evolution of traits 176 to emerge from natural selection generated by the multispecies food web 177 without simplifying the ecology. There is a cost to this in terms of certain 178 assumptions, the most important being a time-scale separation between the 179 ecological and evolutionary dynamics: mutations to the trait have to be 180 infrequent enough for the food web to be at its asymptotic state (typically 181 an equilibrium point) before the next mutant appears. Other assumptions 182 to make the dynamics more tractable include small mutational steps, a 183 simple asexual mutation-selection process (a trait-substitution sequence), 184 and populations that are dominated by a single phenotype at each step. 185

The path of evolution is determined by the initial rate of increase (in-186 vasion fitness) of mutants as they arise in the resident food web. An evo-187 lutionary step starts with the ecological system running to its asymptotic 188 state with a set of resident trait values \mathbf{s} for the species. Having reached 189 this state, a function $\lambda_i(s'_i, \mathbf{s})$ defines the invasion fitness of a mutant with 190 an altered trait value s'_i in species *i*. Despite the complexity of the resident 191 food web, the eigenvalue corresponding to the invasion fitness is found rel-192 atively easily from a Jacobian matrix that contains the mutant dynamics 193 Eq. (B.1) (Appendix B). Evolution of the set of traits is then given by a 194

¹⁹⁵ system of canonical equations, with one equation for each evolving species:

$$\frac{ds_i}{dt} = k_i \frac{\partial}{\partial s'_i} \lambda_i(s'_i, \mathbf{s}) \big|_{s'_i = s_i}$$
(2.2)

¹⁹⁷ (Dieckmann and Law, 1996), where k_i is an evolutionary rate constant for ¹⁹⁸ species *i*. The core information about selection is carried by the partial ¹⁹⁹ derivative of the invasion fitness in the direction of the mutant when the ²⁰⁰ mutant is rare (the selection gradient). What happens if the mutant in-²⁰¹ creases would seem to be left unanswered by this, but a theorem gives the ²⁰² conditions under which invasion implies fixation of the mutant, and these ²⁰³ conditions apply quite widely (Geritz et al., 2002).

²⁰⁴ 2.3 Strength of directional selection from fishing

To examine some basic effects of selective fishing we took just two interact-205 ing fish species from the general framework above, and allowed evolution of 206 one trait on one of them. The evolving trait was the asymptotic body mass 207 w_{∞} , and the mass at 50 % maturation w_m was assumed to be a fixed pro-208 portion of this, so that the whole reproductive schedule would move with 209 body size as the trait evolved. This is in keeping with the similar length ra-210 tios l_m/l_{∞} observed in similar-shaped fish species, in taxonomically related 211 fish species, and in different populations of single species, despite substan-212 tial variation in l_{∞} (Beverton, 1992; Froese and Binohlan, 2000). (As only 213 one species is evolving, the species index is omitted below.) 214

In an evolving system as simple as this, the invasion-fitness surface 215 $\lambda(w'_{\infty}, w_{\infty})$ is enough to show the qualitative outcome of evolution. An 216 example is given in Fig. 3: the surface is saddle-like, and has a singular 217 point of evolution w_{∞}^* at which the selection gradient in Eq. (2.2) is zero. 218 The singular point can be seen by taking a section through through the 219 surface at $\lambda = 0$ known as the pairwise invasibility plot (PIP) (Fig. 3); the 220 singular point is at the intersection of the two lines (Geritz et al., 1998; 221 Brännström et al., 2013). In the system described below, the asymptotic 222 mass evolved to this point and came to rest there. Thus, in this instance, 223 the singular point is a continuously stable strategy (CSS), i.e. an evolu-224 tionarily stable strategy (ESS) (Smith and Price, 1973), to which there 225 is convergence through evolution (Geritz et al., 1998; Brännström et al., 226 2013). We take w_{∞}^* as the trait value of the evolved ancestral population, 227 prior to the introduction of fishing. 228

FIGURE 3 NEAR HERE

196

When fishing mortality is added, the shape of the invasion-fitness surface is distorted, and the singular point at w_{∞}^* becomes invadable by mutants. Some examples are shown in Fig. 4a. The gradient at w_{∞}^* clearly depends on the fishing mortality, and shows the strength of selection generated by fishing. Thus we measure the strength of directional selection S as the slope at the singular point w_{∞}^* :

$$S = \frac{\partial}{\partial \log w'_{\infty}} \lambda(w'_{\infty}, w_{\infty}) \big|_{w'_{\infty} = w^*_{\infty}}, \qquad (2.3)$$

to compare the selective effects of different patterns of exploitation below. (Fig. 3 shows the direction along which the slope is measured.) If the slope becomes negative when fishing is introduced, mutants with smaller w_{∞} can invade, and those with larger w_{∞} cannot; steeper this slope, the greater the selective advantage of these mutants.

In due course, a new mortality regime would cause evolution to another 242 phenotypic state. However, it would be inadvisable to use a simple AD 243 model to investigate this. The strong selection generated by fishing would 244 violate the time-scale separation between ecological and evolutionary dy-245 namics assumed in the AD model. Other methods avoiding this assump-246 tion would be preferred, such as quantitative-genetic and ecogenetic models 247 (Andersen and Brander, 2009; Dunlop et al., 2009). AD in this paper is 248 used just to construct an ancestral singular point of evolution, and to mea-249 sure the strength of selection generated by patterns of fishing mortality at 250 that singular point. 251

FIGURE 4 NEAR HERE

236

253 **3** Numerical results

²⁵⁴ 3.1 Ancestral singular point of evolution

For numerical analysis, we took an ecological system similar to that of Law 255 et al. (2016), comprising a fixed plankton spectrum, together with two fish 256 species, one growing to a small size, and the other to a large size (notionally 257 mackerel and cod). The parameter values specifying the ecological system 258 are given in Appendix C. Some effects of different fishing regimes on this 259 and simpler systems in the absence of evolution have been shown in earlier 260 papers (Law et al., 2015, 2016), but an evolutionary model is needed to 261 examine the strength of selection generated by different fishing methods. 262

²⁶³ Cod was taken as the evolving species, and the evolving trait was w_{∞} ²⁶⁴ with the 50 % maturation as a fixed proportion, 1/15 of w_{∞} . A singular ²⁶⁵ point of evolution of the ancestral cod was found at $w_{\infty}^* \approx 85$ kg (Fig. 3),

near the size of the largest cod ever recorded (Kolding personal communi-266 cation). Equivalently, mass at 50 % maturity w_m^* was 5.67 kg. Predation 267 by mackerel on small cod was the main driver of late maturation in cod in 268 our numerical model, and the strength of predation was therefore tuned to 269 obtain the ancestral value (Appendix C). (In the absence of mackerel, evo-270 lution of the ancestral cod would bring cod to a singular point of evolution 271 at $w_{\infty}^* = 27$ kg in our numerical analysis (results not shown).) The large 272 asymptotic mass and longevity of ancestral cod can be interpreted as an 273 evolutionary outcome of the escape that this gives from heavy predation 274 early in life (Williams, 1966, p.89-91). 275

The invulnerability of the ancestral cod at $w_{\infty}^* \approx 85$ kg in the absence of fishing is evident from the section through the invasion-fitness surface in the direction of the mutant at w_{∞}^* (Fig. 4a, heavy dotted curve). This line reaches its maximum value of zero at w_{∞}^* : in other words, w_{∞}^* is an ESS, uninvadable by any mutant with another trait value w'_{∞} in its neighbourhood. The point w_{∞}^* is taken as the state to which cod evolved prior to the introduction of fishing.

²⁸³ 3.2 Patterns of fishing mortality

We considered three ways in which to distribute fishing mortality rate over 284 body size (Fig. 5). (1) Balanced harvesting (BH) sets the rate to be 285 proportional to the current rate of somatic production at each size, from 286 some minimum size of capture onwards (see Appendix D). (2) Size-at-entry 287 (SAE) fishing has a minimum capture size above which the fishing mortality 288 is constant irrespective of body size. (3) Slot fishing has constant fishing 289 mortality like SAE, but has an additional a maximum body size above 290 which fish are not caught. Each fishing pattern has a parameter controlling 291 the overall intensity of fishing. Under SAE and slot fishing, this is the 292 fishing mortality rate, F, within the exploited size range. Under BH, F is 293 a function of body size, and the parameter is a constant of proportionality 294 c (units: $m^3 g^{-1}$) between the production rate and the fishing mortality at 295 a given body mass. 296

²⁹⁷ FIGURE 5 NEAR HERE

Thus the fishing patterns differ in the fishing mortality above some minimum size of capture (assumed to be knife-edge). Notice that the fall in somatic growth rate and biomass, which typically happens when fish become large for their species, has the effect of making the somatic production rate decrease. This is therefore accompanied by a corresponding fall in fishing mortality under BH. The different fishing patterns distort the ³⁰⁴ invasion-fitness surface (Fig. 3) in different ways, generating different se-³⁰⁵ lection gradients, which will be described below.

The key to understanding the selection on cod generated by fishing is 306 through the changing regime of mortality on cod that fishing brings about. 307 This comes in two parts. First, there is a direct effect on mortality from the 308 fish that are caught. Second, hidden beneath this, are changes in intrinsic 309 mortality, predation mortality and cannibalism inside the size-structured 310 food web, as it adjusts to the fishing. The ecological size-spectrum dynam-311 ics automatically keep track of these internal changes, and the effects of 312 the changes are felt by non-target as well as by target species. 313

314 3.3 Mortality from mackerel predation

The hidden effects of predation are important. For instance, mackerel is not a passive partner in the evolution of cod: predation by mackerel is part of the mortality experienced by cod. If mackerel are harvested, the predation by mackerel on cod is reduced, and this leaves a footprint on the invasion fitness of mutants w'_{∞} in cod, favouring those with lower w'_{∞} (Fig. 4a, dash-dot line), irrespective of any fishing on cod.

We assumed a fixed background of fishing on mackerel, harvested as 321 a SAE fishery with a fishing mortality rate 0.5 yr^{-1} starting at a body 322 mass 250 g. We did this because cod could be seriously depleted by the 323 combined effects of heavy fishing and predation from mackerel, if the latter 324 was unexploited. So fishing on mackerel here was taken as a fixed part 325 of the environment of cod, and was not balanced to match fishing on cod 326 (cf. Law et al., 2016). The selection gradients on cod under fishing should 327 therefore be taken relative to the selection gradient on cod already caused 328 by catching mackerel. However, the impact on cod of fishing mackerel at 329 this level is relatively small, as shown in Fig. 4a. 330

331 3.4 Selection in BH and SAE fisheries

A BH fishery on cod leads to much less selection on the life history than a 332 SAE fishery (Fig. 4a: continuous and dashed lines). This can be seen from 333 the much steeper gradient in the invasion fitness under SAE (continuous 334 curve) than under BH (dashed curve), and is consistent with the prediction 335 that BH is relatively benign in its effects on FIE. Depending on whether 336 the selective effect of fishing mackerel is allowed for, the selection gradient 337 in the SAE fishery is from about five to twenty times that in the BH fishery 338 at the same biomass yield. Fig. 4b extends the comparison of BH and SAE 339

fisheries to show the relation between selection gradient and biomass yield as cod fishing mortality increases from zero (the fishing mortality rate on mackerel is fixed throughout). The major benefits from BH in reducing selection are clear. Note that the selection gradient on cod is negative even when there is no fishing on cod, because mackerel fishing automatically changes the pattern of predation on cod.

Fig. 6 gives a sensitivity analysis of the effect of varying fishing pressure 346 over a range of minimum capture sizes. This confirms the much weaker se-347 lection in BH than in SAE fisheries as the minimum capture size is varied: 348 for a given biomass yield, the selection gradient is substantially closer to 349 zero in BH than in SAE fishing. Yield rises to a peak as fishing increases 350 and then falls until extinction occurs. BH gives the greatest benefits to re-351 ducing selection with moderate levels of fishing, well before the maximum 352 yield is reached. The yield does not return smoothly to zero as fishing 353 increases; instead there is a threshold when the combined effects of fish-354 ing, cannabilism, and predation by mackerel reach a point at which cod 355 collapses. 356

357 FIGURE 6 NEAR HERE

The main benefit of BH comes from bringing fishing in line with pro-358 duction rates of large (not small) fish. This is evident from the fact that 359 the minimum capture sizes in the BH fisheries in Fig. 6a have relatively 360 little effect on the selection gradients as the biomass yield is growing. In 361 contrast, in the SAE fisheries (Fig. 6b), selection for earlier maturation 362 becomes stronger (i.e., S becomes more negative), as fishing becomes more 363 concentrated on adults. In the BH fisheries, the selection gradients in fact 364 get slightly closer to zero as the minimum capture size increases (Fig. 6a), 365 thereby countering the effect of mackerel fishing. 366

367 3.5 Selection in slot fisheries

A detailed balancing of fishing to production rate by species and body size 368 would be hard to achieve in practice. Evidently, low fishing mortality on 369 the big fish that have low production rates is the key to reducing fisheries-370 induced selection on the reproduction schedule. We therefore examined the 371 sensitivity of selection to a range of slot fisheries, as a first approximation 372 to BH (Fig. 7), using two fixed ratios of maximum/minimum capture 373 size of 5 and 10. Like BH and SAE, the yield rises to a peak as fishing 374 increases. But unlike BH, the extinction point can be close to the peak 375 unless the minimum capture size is large. Since collapse could occur with 376 little warning, slot fisheries on small fish would need to be implemented 377

378 with care.

379 FIGURE 7 NEAR HERE

The effect of sliding the slot fisheries across the life history of cod is 380 consistent with a basic notion of life-history theory, that organisms evolve 381 to avoid states where they are at their most vulnerable (Williams, 1966). 382 When small cod are caught (minimum capture sizes: 30, 100, 300 g), the 383 ancestral advantage in large body size as an escape from predation weakens 384 and, as in BH, relatively weak selection for earlier maturation occurs. Such 385 fishing is undoing part of the ancestral selection pressure for late matura-386 tion. When intermediate-sized cod are caught (minimum capture size: 1 387 kg), delayed maturation allows faster growth through the vulnerable size 388 range, pushing the selection gradient a little in the opposite direction, even 389 to the point of reversing the direction of selection (Fig. 7b). When large 390 cod are caught (minimum capture size: 3 kg), delaying maturation carries 391 the heavy cost of potentially not reproducing at all, and, as in SAE fishing, 392 there is strong selection for early maturation. 393

The reversal of fisheries-induced selection is remarkable (Fig. 7b, fishing 394 from 1 to 10 kg). We interpret it in part as an interaction with the mackerel 395 fishery, since this slot size range would include cod that would otherwise 396 be eating the exploited size range of mackerel to a major degree. Catching 397 these cod thus allows more of these mackerel to escape predation, despite 398 the fishery on them (and also more escape from predation by cod of a 399 similar size). The outcome is heavier predation on cod still earlier in life, 400 and overall selection for later maturation. 401

$_{402}$ 4 Discussion

Our results support the prediction that BH is a good deal more benign 403 than traditional SAE fisheries as a selective pressure on the life histories of 404 fish. This is contingent on fishing mortality being set at a moderate level. 405 Although the ecological context of multispecies size spectra is different from 406 previous work, the basic feature, that organisms evolve not to linger in 407 vulnerable states, is congruent with earlier work on life-history evolution 408 (Williams, 1966; Edley and Law, 1988), suggesting a robustness of the 409 results that goes beyond particular model structures. The simple message 410 is that, to keep fishing-induced selection small, it helps to protect big fish 411 with low production rates. 412

Importantly, BH is as much about *reducing* fishing on components of ecosystems that have low production, as it is about fishing on those that

have high production. Fish that are big for their species typically have 415 relatively low somatic production rates, (a) because they have low mass-416 specific somatic growth rates, and (b) because a history of fishing tends to 417 truncate size structures, leaving the remaining big fish with low biomass 418 densities. The somatic production rate is simply the product (a) \times (b), 419 and BH therefore calls for correspondingly little fishing on these big fish. 420 BH thus aligns with a major stream of thinking that big, old fish need 421 protection both for ecological and for evolutionary reasons (Beamish et al., 422 2006; Hsieh et al., 2006, 2010; Hixon et al., 2014). BH contributes to this 423 literature in suggesting somatic production rate as a quantitative guide for 424 setting relative levels of fishing mortality. 425

A precise balancing of fishing mortality to production rate by body 426 size would be hard to achieve in practice. Slot fisheries that select an 427 intermediate range of body size resemble BH at a qualitative level, as they 428 create a refuge for large fish. Our results on fisheries-induced selection 429 caused by slot fishing are consistent with those of a recent study on the 430 use of gillnets in NE Arctic cod (Zimmermann and Jørgensen, 2017). Slot 431 fishing deserves attention in the drive for increased selectivity to reduce 432 discarding (Common Fisheries Policy reform EU Regulation 1380/2013). 433 Selectivity *per se* is not the issue—it is what is being selected that matters. 434 To get the evolutionary benefits from slot fisheries, their upper limits should 435 not extend too far into adult life, as that would generate a strong selective 436 advantage for early reproduction. Slot fisheries involving juveniles have to 437 be implemented with caution because of the clear danger that stocks could 438 collapse from over-exploitation. 439

Taking a multispecies, size-spectrum model as the ecological input into 440 a model of AD provides a new route into life-history evolution and FIE. It 441 deals internally with all the density-dependent growth and mortality gener-442 ated by predation and cannibalism in the size-structured, food-web model. 443 In this way, it removes an artificial separation of natural mortality from 444 fishing mortality. This has some interesting consequences. For instance, 445 it shows how fishing on one species generates selection on another (unex-446 ploited) species, as the food web adjusts to the fishing. It also shows that a 447 fishing regime, appropriately chosen, could change the predation mortality 448 generated within the food-web, reversing the direction of selection caused 449 by fishing. This would be system specific, and would require a detailed un-450 derstanding of how the food web works. The framework we have developed 451 offers a route to exploring the selection pressures generated by fishing on 452 multiple species within a marine ecosystem. 453

Quite apart from the context of FIE, coupling size-spectrum dynamics to
 AD should facilitate research into broader issues about evolution in aquatic

food webs. Current models of size spectrum dynamics contain a number of parameters that could be evolutionary variables, such as how far down the food web predators are feeding, how broad their diets are, and how active they are. Further ecological parameters are likely to become part of the language of size-spectrum models as the research field develops, and AD provides a flexible framework for studying their evolution.

One general evolutionary issue is whether there is a simple maximisation 462 principle at work. Such a principle, that species evolve to reproduce at the 463 body size at which cohort biomass is greatest, has been suggested 464 by Froese et al. (2016) as an argument for the implausability of peaks in 465 biomass at small body size (Law et al., 2016). Our evolutionary analysis 466 does not support this maximum-biomass principle: irrespective of biomass 467 peaks, predation by mackerel on small cod generates an advantage for late 468 maturation in cod. Peaks and troughs in cohort biomass (and equivalently 469 somatic production rate) occur at body sizes where mass-specific growth 470 rate and death rate intersect (Law et al., 2016, Appendix E). These rate 471 functions are nonlinear and rather labile as they are strongly affected by 472 the prevailing predation in the food web. We would therefore expect the 473 peaks of cohort biomass to move around during the course of evolution. 474 Until more is known about such evolution, it is probably sensible to keep 475 an open mind about where peaks in cohort biomass are located with respect 476 to body size, and to try to understand more about the location of peaks 477 from empirical work. 478

Among the caveats about this study is the reduction of the life history 479 to a single scalar measure of reproduction, to allow the whole reproduction 480 schedule to shift to smaller or larger body sizes. This allows some basic 481 calculations, but it simplifies the multidimensional, phenotypic structure of 482 the life history. For instance, there is special interest in probabilistic matu-483 ration reaction norms (PMRNs) as sensitive indicators of FIE (Heino et al., 484 2002; Heino and Dieckmann, 2008). The ecological, size-spectrum dynam-485 ics do carry dependence of growth on food, so there is an implied PMRN, 486 which would be seen as prey densities change; this PMRN would depend 487 on age (not body size) with the size-spectrum model as implemented here. 488

A second caveat is that we have not dealt with the rate at which FIE 489 takes place. This is because it would be hard to justify AD's time-scale 490 separation between ecological and evolutionary dynamics in contemporary 491 fisheries. Our results say only that, for a given biomass yield, the strength 492 of selection could be brought down by roughly an order of magnitude by 493 moving from SAE fishing to BH and appropriate slot fisheries. The rate of 494 evolutionary change caused by fishing is widely discussed (e.g. Jørgensen 495 et al., 2007; Andersen and Brander, 2009; Audzijonyte et al., 2013a; Heino 496

et al., 2015), but has not gained traction in the practical management of fisheries. This is unfortunate because the longer, decadal time-scale of FIE does not absolve managers of marine ecosystems from responsibility for such changes. One reason for linking FIE to BH is that, as well as helping to resolve some short-term issues, BH can evidently also assist conservation of fish stocks in the longer term.

A third caveat is that fishing gear obviously has many selective effects other than changing the mortality rate, for instance on behaviour or reproductive phenology (Heino et al., 2015; Andersen et al., 2018; Tillotson and Quinn, 2018). Such selective effects of fishing gear can be quite different from those generated by natural predators. The prediction in this paper is simply about the distribution of mortality on the evolution of life histories under different schemes of fishing.

Our main result, that fisheries-induced selection would be reduced by lowering fishing mortality on fish that are big for their species, should be robust. However the fine details of feedbacks within food webs are bound to be context dependent. Feedbacks in multispecies, size-structured food webs are intricate, and the challenge as fisheries science moves towards an ecosystem approach is to see what, if any, broad robust patterns emerge from the fine details (Audzijonyte et al., 2013b).

517 Acknowledgements

This research received funding from the European Commissions Horizon 518 2020 Research and Innovation Programme under Grant Agreement No. 519 634495 for the project Science, Technology, and Society Initiative to min-520 imize Unwanted Catches in European Fisheries (MINOUW). MJP was 521 partly funded by Te Pūnaha Matatini, a New Zealand Centre of Research 522 Excellence. The work was facilitated by the School of Mathematics and 523 Statistics, University of Canterbury, New Zealand, which hosted a research 524 visit by RL. Gustav Delius and Richard Southwell gave advice on imple-525 menting the fast Fourier transform. 526

527 **References**

- Andersen, K. H. and Beyer, J. E. (2006). Asymptotic size determines
 species abundance in the marine size spectrum. *American Naturalist*, 168:54–61.
- Andersen, K. H., Blanchard, J. L., Fulton, E. A., Gislason, H., Jacobsen,
 N. S., and van Kooten, T. (2016). Assumptions behind size-based ecosystem models are realistic. *ICES Journal of Marine Science*, 73:1651–1655.
 doi:10.1093/icesjms/fsv211.
- Andersen, K. H. and Brander, K. (2009). Expected rate of fisheries-induced
 evolution is slow. *Proceedings of the National Academy of Sciences USA*, 106:11657–11660. doi:10.1073pnas.0901690106.
- Andersen, K. H., Marty, L., and Arlinghaus, R. (2018). Evolution of boldness and life history in response to selective harvesting. *Canadian Journal*of Fisheries and Aquatic Sciences, 75:271–281. dx.doi.org/10.1139/cjfas2016–0350.
- Audzijonyte, A., Kuparinen, A., and Fulton, E. A. (2013a). How
 fast is fisheries-induced evolution? quantitative analysis of modelling and empirical studies. *Evolutionary Applications*, 6:585–595.
 doi:10.1111/eva.12044.
- Audzijonyte, A., Kuparinen, A., Gorton, R., and Fulton, E. A. (2013b).
 Ecological consequences of body size decline in harvested fish species:
 positive feedback loops in trophic interactions amplify human impact. *Biology Letters*, 9:20121103. doi:10.1098/rsbl.2012.1103.
- Beamish, R. J., McFarlane, G. A., and Benson, A. (2006). Longevity
 overfishing. *Progress in Oceanography*, 68:289–302. doi:10.1016/
 j.pocean.2006.02.005.
- Beverton, R. J. H. (1992). Patterns of reproductive strategy parameters
 in some marine teleost fishes. *Journal of Fish Biology*, 41 (Supplement B):137–160. doi.org/10.1111/j.1095–8649.1992.tb03875.x.
- ⁵⁵⁶ Blanchard, J. L., Andersen, K. H., Scott, F., Hintzen, N. T., Piet, G., and
 ⁵⁵⁷ Jennings, S. (2014). Evaluating targets and trade-offs among fisheries
 ⁵⁵⁸ and conservation objectives using a multispecies size spectrum model.
 ⁵⁵⁹ Journal of Applied Ecology, 51:612–622. doi:10.1111/1365–2664.12238.
- Brännström, Å., Johansson, J., and von Festenberg, N. (2013). The hitchhikers guide to adaptive dynamics. *Games*, 4:304–328. doi:10.3390/
 g4030304.

- Chebib, J., Renaut, S., Bernatchez, L., and Rogers, S. M. (2016). Genetic
 structure and within-generation genome scan analysis of fisheries-induced
 evolution in a lake whitefish (*Coregonus clupeaformis*) population. *Conservation Genetics*, 17:473–483. doi:10.1007/s10592–015–0797–y.
- ⁵⁶⁷ Conover, D. O. and Munch, S. B. (2002). Sustaining fisheries yields over
 ⁵⁶⁸ evolutionary time scales. *Science*, 297:94–96.
- Datta, S., Delius, G. W., and Law, R. (2010). A jump-growth model for predator-prey dynamics: derivation and application to marine ecosystems. *Bulletin of Mathematical Biology*, 72:1361–1382. doi:10.1007/s11538-009-9496-5.
- Datta, S., Delius, G. W., Law, R., and Plank, M. J. (2011). A stability
 analysis of the power-law steady state of marine size spectra. *Journal of Mathematical Biology*, 63:779–799. doi:10.1007/s00285-010-0387-z.
- ⁵⁷⁶ Dieckmann, U. and Law, R. (1996). The dynamical theory of coevolution: a
 derivation from stochastic ecological processes. *Journal of Mathematical Biology*, 34:579–612.
- ⁵⁷⁹ Dunlop, E. S., Heino, M., and Dieckmann, U. (2009). Eco-genetic modeling
 ⁵⁸⁰ of contemporary life-history evolution. *Ecological Applications*, 19:1815–
 ⁵⁸¹ 1834.
- Edley, M. T. and Law, R. (1988). Evolution of life histories and yields in
 experimental populations of *Daphnia magna*. *Biological Journal of the Linnean Society*, 34:309–326.
- Eikeset, A. M., Dunlop, E. S., Heino, M., Storvik, G., Stenseth, N. C.,
 and Dieckmann, U. (2016). Roles of density-dependent growth and life
 history evolution in accounting for fisheries-induced trait changes. *Proceedings of the National Academy of Sciences USA*, 113:15030–15035.
 doi:10.1073/pnas.1525749113.
- Enberg, K. and Jørgensen, C. (2017). Conclusion that fishing-induced
 evolution is negligible follows from model assumptions. *Proceedings of the National Academy of Sciences USA*, 114:. doi:10.1073/pnas.1700708114.
- Froese, R. and Binohlan, C. (2000). Empirical relationships to estimate
 asymptotic length, length at first maturity and length at maximum yield
 per recruit in fishes, with a simple method to evaluate length frequency
 data. Journal of Fish Biology, 56:758–773. doi:10.1006/jfbi.1999.1194.

Froese, R., Walters, C., Pauly, D., Winker, H., Weyl, O. L. F., Demirel, N.,
Tsikliras, A. C., and Holt, S. J. (2016). A critique of the balanced harvesting approach to fishing. *ICES Journal of Marine Science*, 73:1640–
1650. doi:10.1093/icesjms/fsv122.

Garcia, S. M., Kolding, J., Rice, J., Rochet, M.-J., Zhou, S., Arimoto,
T., Beyer, J. E., Borges, L., Bundy, A., Dunn, D., Graham, N., Hall,
M., Heino, M., Law, R., Makino, M., Rijnsdorp, A. D., Simard, F., and
Smith, A. D. M. (2012). Reconsidering the consequences of selective
fisheries. *Science*, 335:1045–1047.

Geritz, S. A. H., Gyllenberg, M., Jacobs, F. J. A., and Parvinen, K. (2002).
 Invasion dynamics and attractor inheritance. *Journal of Mathematical Biology*, 44:560–560. doi:10.1007/s002850100136.

Geritz, S. A. H., Kisdi, E., Meszéna, G., and Metz, J. A. J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of
the evolutionary tree. *Evolutionary Ecology*, 12:35–57.

Hartvig, M., Andersen, K. H., and Beyer, J. E. (2011). Food web framework
for size-structured populations. *Journal of Theoretical Biology*, 272:113–
122. doi:10.1016/j.jtbi.2010.12.006.

Haugen, T. O. and Vøllestad, L. A. (2001). A century of life-history evolution in grayling. *Genetica*, 112113:475–491.

Heath, M., Law, R., and Searle, K. (2017). Scoping the background information for an ecosystem approach to fisheries in scottish waters: Review of predator-prey interactions with fisheries, and balanced harvesting. Technical report, A study commissioned by Fisheries Innovation
Scotland (FIS). ISBN: 978-1-911123-10-1, www.fiscot.org.

Heino, M. and Dieckmann, U. (2008). Detecting fisheries-induced lifehistory evolution: an overview of the reaction norm approach. *Bulletin*of Marine Science, 83:69–93.

Heino, M., Dieckmann, U., and Godø, O. R. (2002). Measuring probabilistic reaction norms for age and size at maturation. *Evolution*, 56:669–678.

Heino, M., Pauli, B. D., and Dieckmann, U. (2015). Fisheries-induced
evolution. Annual Review of Ecology and Systematics, 46:461–480.
doi:10.1146/annurev–ecolsys–112414–054339.

Hixon, M. A., Johnson, D. W., and Sogard, S. M. (2014). BOFFFFs:
on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, 73:1623–1631.
doi:10.1093/icesjms/fst200.

- Hsieh, C.-h., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M.,
 and Sugihara, G. (2006). Fishing elevates variability in the abundance
 of exploited species. *Nature*, 443:859–862. doi:10.1038/nature05232.
- Hsieh, C.-h., Yamauchi, A., Nakazawa, T., and Wang, W.-F. (2010). Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, 72:165–178. doi:10.1007/s00027–009–0122–2.
- Jacobsen, N. S., Gislason, H., and Andersen, K. H. (2014). The consequences of balanced harvesting of fish communities. *Proceedings of the Royal Society B*, 281:20132701. doi:0.1098/rspb.2013.2701.
- Jennings, S., Pinnegar, J. K., Polunin, N. V. C., and Boon, T. W. (2001).
 Weak cross-species relationships between body size and trophic level belie
 powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, 70:934–944.
- Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S.,
 Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S.,
 Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M.,
 and Rijnsdorp, A. D. (2007). Managing evolving fish stocks. *Science*,
 318:1247-1248. doi:10.1126/science.1148089.
- Kisdi, É. and Geritz, S. A. H. (2010). Adaptive dynamics: a framework
 to model evolution in the ecological theatre. *Journal of Mathematical Biology*, 61:165–169. doi:10.1007/s00285–009–0300–9.
- Kolding, J., Bundy, A., van Zwieten, P. A. M., and Plank, M. J. (2016a).
 Fisheries, the inverted food pyramid. *ICES Journal of Marine Science*, 73:1697–1713. doi:10.1093/icesjms/fsv225.
- Kolding, J., Jacobsen, N. S., Andersen, K. H., and van Zwieten, P. A. M.
 (2016b). Maximizing fisheries yields while maintaining community structure. *Canadian Journal of Fisheries and Aquatic Sciences*, 73:644–655.
 doi:10.1139/cjfas-2015-0098.
- Law, R. (2007). Fisheries-induced evolution: present status and future directions. *Marine Ecology Progress Series*, 335:271–277.
- Law, R., Kolding, J., and Plank, M. J. (2015). Squaring the circle: reconciling fishing and conservation of aquatic ecosystems. *Fish and Fisheries*,
 16:160–174. doi:10.1111/faf.12056.
- Law, R., Plank, M. J., and Kolding, J. (2012). On balanced exploitation
 of marine ecosystems: results from dynamic size spectra. *ICES Journal* of Marine Science, 69:602–614. doi:10.1093/icesjms/fss031.

Law, R., Plank, M. J., and Kolding, J. (2016). Balanced exploitation
and coexistence of interacting, size-structured, fish species. *Fish and Fisheries*, 17:281–302. doi:10.1111/faf.12098.

Metz, J. A. J., Geritz, S. A., Meszéna, G., Jacobs, F. J., and Heerwaarden,
J. V. (1996). Adaptive dynamics, a geometrical study of the consequences
of nearly faithful reproduction. In van Strien, S. J. and Verduyn Lunel,
S. M., editors, *Stochastic and Spatial Structures of Dynamical Systems*,
pages 183–231. North-Holland Publishing Co, Amsterdam, The Netherlands.

Metz, J. A. J., Nisbet, R. M., and Geritz, S. A. H. (1992). How should
we define fitness for general ecological scenarios? *Trends in Ecology and Evoution*, 7:198–202. doi.org/10.1016/0169–5347(92)90073–K.

Silvert, W. and Platt, T. (1978). Energy flux in the pelagic ecosystem: a
 time-dependent equation. *Limnology and Oceanography*, 23:813–816.

Sinko, J. W. and Streiffer, W. (1971). A model for populations reproducing
 by fission. *Ecology*, 52:330–335.

Smith, J. M. and Price, G. (1973). The logic of animal conflict. *Nature*, 246:15–18.

Tillotson, M. D. and Quinn, T. P. (2018). Selection on the timing of
migration and breeding: a neglected aspect of fishing-induced evolution
and trait change. *Fish and Fisheries*, 19:170–181. doi:10.1111/faf.12248.

van Wijk, S. J., Taylor, M. I., Creer, S., Dreyer, C., Rodrigues, F. M.,
Ramnarine, I. W., van Oosterhout, C., and Carvalho, R. (2013). Experimental harvesting of fish populations drives genetically based shifts in
body size and maturation. *Frontiers in Ecology and the Environment*,
11:181–187. doi:10.1890/120229.

Williams, G. C. (1966). Adaptation and Natural Selection. Princeton Uni versity Press Princeton.

Zimmermann, F. and Jørgensen, C. (2017). Taking animal breeding
into the wild: regulation of fishing gear can make fish stocks evolve
higher productivity. *Marine Ecology Progress series*, 563:185–195.
doi:10.3354/meps11996.

702 Tables

Parameter	Mackerel	Cod	Unit	Comments
				Fich life histories.
$au c^{x_i} 0$	0.001	0.001	۲.	Fish life histories:
$w_0 e^{x_{i,0}}$	0.001		g	mass of fish egg
$w_0 e^{x_i,m}$	200	evolving	g	mass at 50% maturity
$w_0 e^{-i,\infty}$	000	evolving	g	asymptotic mass
$ ho_{i,m}$	61	8	—	controls the body-size range over
	0.0	0.0		which maturation occurs
ρ	0.2	0.2	_	exponent for approach to asymp-
				totic body size in reproduction
				funcion
				-
				Dynamic size spectra of fish
				species:
K	0.2	0.2	_	food conversion efficiency
$lpha_i$	0.8	0.8	_	search rate scaling exponent
A_i	750	700	$\mathrm{m}^3 \mathrm{yr}^{-1} \mathrm{g}^{-\alpha}$	feeding rate constant
β_i	6	4.5	_	natural log of mean predator prey
				mass ratio
σ_i	2.5	1.9	_	diet breadth
$\mu_{oi}^{(0)}$	0.1	0.1	$\rm yr^{-1}$	intrinsic mortality rate at birth
ξ	-0.15	-0.15	_	exponent for intrinsic mortality
				Fixed plankton size spectrum:
$w_0 e^{x_{0,min}}$	4.8×10^{-11}		g	lowest body mass of plankton
$w_0 e^{x_{0,max}}$	0.03		g	greatest body mass of plankton
$u_{0,0}$	100		${ m m}^{-3}$	plankton density at 1 mg
γ	2		_	exponent of plankton spectrum

Table 1: Model parameters and values.

Figure legends



Figure 1: Road map of modelling steps. Boxes are cartoons of size spectra; with two species (filled and empty), and shapes depicting different phenotypes. The ecological model is run to determine the equilibrium state of the two species (STEP 1). New phenotypes are generated by mutation (STEP 2). The fate of a new phenotype is decided by the ecological dynamics (STEP 1). These steps are iterated as shown by the arrows until eventually the system reaches a state at which no further mutant can invade, an evolutionarily stable state (ESS). Contemporary fishing at this ancestral ESS generates new selection on the life history (STEP 3). The paper contrasts the strength of selection generated by balanced harvesting (BH) with size-at-entry and slot fishing.



Figure 2: Processes acting on fish of body mass w. Growth comes from feeding on smaller fish of the same and other species, given by rate term (a) in Eq. (2.1). The main cause of death is predation and cannibalism by larger fish, a component of the rate term (b) in Eq. (2.1). Feeding is set by a preference function for prey relative to size w, determined by a species-specific predator:prey mass ratio. Heavy lines are examples of size spectra on log-log axes; these lines can change in shape over the course of time, as fish grow and die. Dashed lines show biomass flows from prey to predator.



Figure 3: An example of an invasion fitness surface λ for a mutant with trait value w'_{∞} as it enters a resident population with trait value w_{∞} , and its corresponding pairwise invasibility plot (PIP), the section through the surface at $\lambda = 0$. Filled circles mark the singular point of evolution, w^*_{∞} . Signs show the sectors of the PIP in which the invasion fitness of mutants is positive and negative, with boundaries given by the dash-dot line. The dotted line shows the direction in which selection gradient, Eq. (2.3), is measured.



Figure 4: Invasion fitnesses and selection gradients S of cod mutants, under fishing schemes defined in the text. (a) Sections through invasion-fitness surfaces λ in the mutant direction w'_{∞} at w^*_{∞} (the direction of the dotted line in Fig. 3). The ancestral, unexploited system has a singular point of evolution w_{∞}^* at 85 kg (S = 0). The selection gradient on cod from fishing is measured by the gradient S at w_{∞}^* , Eq. (2.3), as shown in the inset. Fishing mackerel, and not cod, leads to some selection on cod: $S = -0.0051 \text{ yr}^{-1}$. Adding balanced harvesting (BH) on cod to the background fishing of mackerel, slightly increases selection on cod: $S = -0.0067 \text{ yr}^{-1}$ (cod minimum capture size 100 g, $c = 11.0 \text{ m}^3 \text{ g}^{-1}$). Adding size-at-entry (SAE) fishing on cod to the background fishing of mackerel, gives much stronger selection on cod: $S = -0.0392 \text{ yr}^{-1}$ (cod minimum capture size 1 kg, $F = 0.2 \text{ yr}^{-1}$). (b) Effects of increasing cod fishing on selection gradients S and biomass yields (minimum capture sizes remain as in (a)). Arrows show the direction of increasing fishing on cod, starting from 0 and ending close to extinction of cod (near $c = 70 \text{ m}^3 \text{ kg}^{-1}$ in the case of BH, and $F = 0.32 \text{ yr}^{-1}$ in the case of SAE). Filled circles mark the selection gradients of the cod BH and SAE fisheries shown in panel (a).



Figure 5: Three kinds of fishing mortality F: balanced harvesting (BH), sizeat-entry (SAE), and slot. Each fishing pattern has a parameter controlling the overall fishing intensity, which moves the fishing mortality rates up or down; here their values are: BH $c = 30 \text{ m}^3 \text{ g}^{-1}$, SAE $F = 0.22 \text{ yr}^{-1}$, slot $F = 0.65 \text{ yr}^{-1}$. These parameter values were chosen to generate biomass yields near to 0.01 g m⁻³ yr⁻¹ at steady state. They give selection gradients S (yr⁻¹): BH -0.008, SAE -0.045, slot -0.014.



Figure 6: Selection gradients S and biomass yields of cod as fishing mortality on cod increases in: (a) balanced harvesting (BH) fisheries; (b) size-at-entry (SAE) fisheries. Each line describes a different minimum capture size, as shown in the keys. Lines end where fishing mortality rate causes extinction of cod; this is close to the value given in brackets, $c \,(\mathrm{m}^3 \,\mathrm{kg}^{-1})$ in the case of BH, and $F \,(\mathrm{yr}^{-1})$ in the case of SAE.



Figure 7: Selection gradients S and biomass yields of cod obtained as fishing mortality on cod increases in slot fisheries: (a) maximum capture size at 5 times the minimum; (b) maximum capture size at 10 times the minimum. Each line describes a different minimum capture size, as shown in the keys. Lines end where fishing mortality rate F causes extinction of cod close to the value (yr⁻¹) given in brackets, except for minimum capture size 30 g, which is off the scale.

704 Appendices

705 A Multispecies dynamics

It is convenient to work in terms of the logarithmic body mass variable, $x = \ln(w/w_0)$, where w_0 is an arbitrary body mass. This gives a state variable $u_i(x,t)dx = \phi_i(w,t)dw$, with dimensions L^{-3} , which corresponds to the density of individuals of type *i* with log body mass in the range x, x + dx at time *t*. 'Type' may be a species or a mutant within a species. The dynamics of $u_i(x)$ are given by the partial differential equation (Law et al., 2016):

$$\frac{\partial u_i}{\partial t} = \underbrace{-\frac{\partial}{\partial x} \left[\epsilon_i g_i u_i\right]}_{\text{for all } i} + \underbrace{\frac{\partial}{2} \frac{\partial}{\partial x} \left[e^{-x} \frac{\partial}{\partial x} \left[\epsilon_i G_i u_i\right]\right]}_{\text{for all } i} + \underbrace{\frac{\partial}{b_i R_i} e^{-x}}_{2} - \underbrace{\frac{\partial}{\mu_{\text{tot},i} u_i}}_{\text{for all } i}, \quad (A.1)$$

where the arguments x and t have been omitted from each function. The 714 functions $g_i(x,t)$, $G_i(x,t)$ and $\mu_{tot,i}(x,t)$ respectively represent the rates of 715 mass-specific prey biomass assimilation, diffusion and mortality for type i716 at log body mass x and time t. The function $R_i(t)$ is the reproduction rate 717 (number of eggs produced per unit volume per unit time) of type i at time 718 t. The function $\epsilon_i(x)$ is the proportion of assimilated prey biomass that is 719 used for somatic growth by individuals of type i and log body mass x. Each 720 of these functions will be defined below. The function $b_i(x)$ represents the 721 mass distribution of eggs of type i. This is assumed to be a Dirac-delta 722 function, corresponding to a unique log mass $x_{i,0}$ for type *i*. Eq. (A.1) is an 723 extension of the size-based McKendrick-von Foerster equation to include 724 a second-order diffusion-like term. This allows for demographic variability 725 in size-at-age trajectories (Datta et al., 2010, 2011), although in practice 726 this is small. 727

The model assumes that a predator of type i and log body mass xsearches a volume of water $A_i e^{\alpha_i x}$ per unit time, and has a relative preference for prey that is given by a function $s_i(r)$ of the predator: prey mass ratio r. The relative encounter rate between individuals of type i and individuals of type j is denoted θ_{ij} . The mass-specific prey biomass assimilation rate $g_i(x)$ is calculated as an integral over the abundance of potential prey:

734
$$g_i(x) = A_i K e^{(\alpha_i - 1)x} \sum_{j=0}^n \theta_{ij} \int e^{x'} s_i(e^{x - x'}) u_j(x') dx'.$$
(A.2)

⁷³⁵ Similarly, the rate function for the second-order diffusion term $G_i(x)$ is

 $_{736}$ given by (Law et al., 2016)

741

744

754

$$G_i(x) = A_i K^2 e^{(\alpha_i - 1)x} \sum_{j=0}^n \theta_{ij} \int e^{2x'} s_i(e^{x - x'}) u_j(x') dx'.$$
(A.3)

Three sources of mortality are included: predation mortality, natural non-predation mortality (referred to as intrinsic mortality) and fishing mortality

$$\mu_{ ext{tot},i}(x) = \mu_i(x) + \mu_{o,i}(x) + \mu_{F,i}(x).$$

The predation mortality rate $\mu_i(x)$ is calculated as an integral over the abundance of potential predators:

$$\mu_i(x) = \sum_{j=1}^n A_j \theta_{ji} \int e^{\alpha_j x'} s_j(e^{x'-x}) u_j(x') dx'.$$
(A.4)

The intrinsic mortality rate $\mu_{o,i}(x)$ accounts for sources of mortality other 745 than predation and fishing. We assume that this is proportional to the 746 mass-specific needs for metabolism, relative to the mass-specific rate at 747 which food becomes available at size x. These rates are set relative to their 748 values at egg size, so $\mu_{o,i}(x_{i,0}) = \mu_{o,i}^{(0)}$ is a fixed baseline intrinsic mortality at 749 birth for type i. The metabolic need should scale with body mass, and we 750 write this as $\exp(-\xi(x-x_{i,0}))$, using the same exponent for all types. The 751 mass-specific prey intake rate at size x relative to size $x_{i,0}$ is $g_i(x)/g_i(x_{i,0})$. 752 Thus 753

$$\mu_{o,i}(x) = \mu_{o,i}^{(0)} \exp(-\xi(x - x_{i,0}))g_i(x_{i,0})/g_i(x), \tag{A.5}$$

which is also a function of time because it depends on the mass-specific prey intake rate $g_i(x)$.

The feeding kernel for type *i* is a Gaussian function of log predator-toprey mass ratio *r*, with mean β_i and standard deviation σ_i . The feeding kernel is assumed to be 0 when r < 1 so that predators are always larger than their prey:

761
$$s_i(r) = \left\{ \begin{array}{ll} \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(\ln(r)-\beta_i)^2}{2\sigma_i^2}\right) & r \ge 1\\ 0 & r < 1 \end{array} \right\}.$$
 (A.6)

The function $\epsilon_i(x)$ the proportion of incoming prey biomass that is allocated to reproduction, using a form suggested by Hartvig et al. (2011):

764
$$1 - \epsilon_i(x) = [1 + \exp(-\rho_{i,m}(x - x_{i,m}))]^{-1} \exp(\rho(x - x_{i,\infty})).$$
(A.7)

Here $w_0 e^{x_{i,m}}$ is the body mass at which 50 % of the fish of type *i* are mature, and $\rho_{i,m}$ defines the body-mass range over which fish are maturing. The ⁷⁶⁷ asymptotic body mass $w_0 e^{x_{i,\infty}}$ is the size at which all incoming mass is ⁷⁶⁸ allocated to reproduction and no further somatic growth is possible, the ⁷⁶⁹ approach to this size being scaled by a parameter ρ common to all types.

The egg size $x_{i,0}$ and asymptotic size $x_{i,\infty}$ together give boundary condi-770 tions for Eq. (A.1), over which there is no flux of individuals. For simplicity, 771 we do not deal with the dynamics of the plankton. This can be thought 772 of as an assumption that the plankton operate on a short timescale rel-773 ative to the fish community. The fixed plankton spectrum was taken as 774 $u_0(x) = u_{0,0} \exp^{(1-\gamma)x}$, where $u_{0,0}$ is the abundance of plankton of mass 1 775 mg, giving a power-law relationship between body mass and abundance. 776 Parameter values are given in Table 1. 777

778 **B** Invasion fitness

We consider a resident community consisting of two species coexisting at a stable equilibrium (though the following easily generalises to more than two species). The discretised version of the size-spectrum model consists of the abundance u_i of each species in size classes x_k (k = 1, ..., N) with step size Δx . The Jacobian matrix of the two-species system takes the form

784
$$\mathbf{J}_{\mathrm{res}} = \left[egin{array}{cc} \mathbf{J}_{11} & \mathbf{J}_{12} \ \mathbf{J}_{21} & \mathbf{J}_{22} \end{array}
ight]$$

where \mathbf{J}_{ij} is the $N \times N$ matrix describing the dependence of species *i* on species *j*. We require that this two-species system has a stable equilibrium in which both species are non-zero, so that all eigenvalues of the Jacobian evaluated at this equilibrium, \mathbf{J}_{res}^* , have negative real part.

Now suppose the community is augmented by a mutant of species 2
indexed 2'. The expanded system has a Jacobian matrix of the form

791
$$\mathbf{J}_{\text{aug}} = \begin{bmatrix} \mathbf{J}_{11} & \mathbf{J}_{12} & \mathbf{J}_{12'} \\ \mathbf{J}_{21} & \mathbf{J}_{22} & \mathbf{J}_{22'} \\ \mathbf{J}_{2'1} & \mathbf{J}_{2'2} & \mathbf{J}_{2'2'} \end{bmatrix}$$

796

The state at which the resident species 1 and 2 are at the two-species equilibrium and the mutant 2' is absent is also an equilibrium of the augmented system. When the Jacobian matrix \mathbf{J}_{aug} is evaluated at this equilibrium, the submatrices $\mathbf{J}_{2'1}$ and $\mathbf{J}_{2'2}$ are zero. Hence the Jacobian is

$$\mathbf{J}_{\text{aug}}^{*} = \begin{bmatrix} \mathbf{J}_{11} & \mathbf{J}_{12} & \mathbf{J}_{12'} \\ \mathbf{J}_{21} & \mathbf{J}_{22} & \mathbf{J}_{22'} \\ 0 & 0 & \mathbf{J}_{2'2'}^{*} \end{bmatrix}$$
(B.1)

The eigenvalues of this matrix consist of the eigenvalues of \mathbf{J}_{res}^* , which all have negative real part, together with the eigenvalues of $\mathbf{J}_{2'2'}^*$, which is $\mathbf{J}_{2'2'}$ evaluated at the coexistence equilibrium of 1 and 2, with 2' at zero.

The elements of the Jacobian $\mathbf{J}_{2'2'}$ can be obtained from the discretised version of the PDE, Eq. (A.1), for the mutant. For brevity, we drop the mutant index by using u_k to denote $u_{2'}(x_k)$, and similarly g_k , G_k , ϵ_k , $\mu_{\text{tot},k}$. The discretised version of the PDE is then:

$$\frac{du_k}{dt} = \frac{\epsilon_{k-1}g_{k-1}u_{k-1} - \epsilon_k g_k u_k}{\Delta x}$$

$$+e^{-x_k}\frac{\epsilon_{k-1}G_{k-1}u_{k-1}+\epsilon_{k+1}G_{k+1}u_{k+1}-2\epsilon_kG_ku_k}{2\Delta x^2}$$

806

805

$$+e^{-x_k}\frac{\epsilon_{k-1}G_{k-1}u_{k-1}-\epsilon_kG_ku_k}{2\Delta x}$$

$$-\mu_{\text{tot},k}u_k + \frac{\delta_{k1}Re^{-x_0}}{\Delta x},$$
 (B.2)

where δ_{kl} is the Kronecker-delta symbol.

From Eq. (B.2), the elements of $\mathbf{J}_{2'2'}^*$ are:

$$a_{kk} = -\frac{\epsilon_k g_k}{\Delta x} - e^{-x_k} \epsilon_k G_k \left(\frac{1}{\Delta x^2} + \frac{1}{2\Delta x}\right) - \mu_{\text{tot},k},$$

$$a_{k,k-1} = \frac{\epsilon_{k-1}g_{k-1}}{\Delta x} + e^{-x_k}\epsilon_{k-1}G_{k-1}\left(\frac{1}{2\Delta x^2} + \frac{1}{2\Delta x}\right),$$

$$a_{k,k+1} = \frac{e^{-x_k}\epsilon_{k+1}G_{k+1}}{2\Delta x^2},$$

$$a_{1k} = \frac{e^{x_k - x_0} (1 - \epsilon_k) g_k}{2}.$$
 (B.3)

All other elements of $\mathbf{J}_{2'2'}^*$ are zero because terms of the form $\partial/\partial u_l(g_k u_k)$ 814 are all zero when evaluated at the equilibrium $u_k = 0$. The functions g_k , 815 G_k and $\mu_{\text{tot},k}$ depend on the resident abundances via Eqs. (A.2)–(A.4). 816 In the special case considered in this model, where the only difference 817 between the mutant 2' and the resident 2 is in its reproduction schedule 818 (ϵ_k) , the functions g_k , G_k and $\mu_{tot,k}$ will be identical to those for the resident 819 2. In other words, the mutant experiences the same size-dependent food 820 intake and mortality rates as the resident, but differs in the proportion of 821 incoming biomass that is allocated to reproduction. In the simpler case 822 of the McKendrick—von Foerster equation without diffusion, the Jacobian 823 elements above omit all terms containing G_k . 824

The two-species coexistence equilibrium is stable to introduction of the mutant (i.e. a rare mutant will die out) if all eigenvalues of $\mathbf{J}_{2'2'}^{*}$ have negative real part. If $\mathbf{J}_{2'2'}^{*}$ has an eigenvalue with positive real part, the two-species equilibrium is unstable to the introduction of the mutant (i.e. a rare mutant will increase in abundance). The eigenvalue with largest real part λ is the rate of increase of the mutant population when the mutant is rare, i.e. the invasion fitness.

⁸³² C Numerical methods

We took a community of two fish species, one growing to a small size, and 833 the other to a large size, together with a fixed plankton spectrum. This 834 was based on Law et al. (2016), the two species having parameter values 835 motivated by mackerel and cod (Table 1) as described in Law et al. (2016). 836 The dynamics were described by Eqns (A.1), with mackerel indexed i = 1, 837 and cod i = 2. The asymptotic body mass of cod, $x_{\infty} = \ln(w_{\infty})$, was set to 838 evolve, and the mass at 50 % maturation, $x_m = \ln(w_m)$, evolved with it as 839 fixed proportion $\ln(1/15)$ of this. The matrix of preferences θ_{ij} of predators 840 of type i for prev of type j was: 841

$$\boldsymbol{\theta} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 1 & 1 & 0.2 & 0.2 \\ 1 & 0.2 & 1 & 1 \\ 1 & 0.2 & 1 & 1 \end{pmatrix}.$$
 (C.1)

842

The first three rows of $\boldsymbol{\theta}$, indexed i = 0, 1, 2, refer respectively to: (0) plankton, (1) mackerel, and (2) cod with resident trait value x_{∞} . The final row refers to predation by mutant cod x'_{∞} , with predation preferences set to be the same as resident cod. The cross-species predation parameters, $\theta_{ij} = 0.2$, were chosen to take cod's x_{∞} to a singular point of ancestral evolution x^*_{∞} near that of the largest recorded cod.

TABLE 1 NEAR HERE

For numerical analysis, the continuous equations were discretized to 850 a system of ordinary differential equations using as small a step size as 851 practicable ($\Delta x = 0.05$). For given parameter values, we obtained a close 852 approximation to the steady state from a numerical integration over a 100 853 yr time period, using a time step $\Delta t = 0.0005$, based on the Euler method. 854 The Gaussian feeding kernel $s_i(r)$ Eq. (A.6) was truncated at $\pm 3\sigma$, and 855 normalised to sum to 1. Fast Fourier transforms were used to compute 856 the convolution integrals. In cases where convergence to the steady state 857 was slow, the time period of integration was extended. We terminated 858 sequences of increasing fishing mortality at extinction of the cod. 859

Having reached the steady state of an arbitrary resident community (with cod's trait value at x_{∞}), we constructed the life history of a rare mutant with an altered trait value x'_{∞} . The Jacobian matrix of the resident community, augmented by the rare mutant, could then be built, with elements as given in Eqs (B.3). The invasion fitness, $\lambda(x'_{\infty}, x_{\infty})$, of the mutant cod in the resident community is the real part of the leading eigenvalue of this matrix.

A singular point of evolution x_{∞}^* occurs at

$$0 = \frac{\partial}{\partial x'_{\infty}} \lambda(x'_{\infty}, x_{\infty}) \big|_{x'_{\infty} = x_{\infty}},$$
(C.2)

obtained numerically from a pairwise invasibility plot, using a grid of values $(x'_{\infty}, x_{\infty})$ of invasion fitness (Fig. 3). The strength of directional selection generated by fishing on cod at the singular point x^*_{∞} , was measured as

$$S = \frac{\lambda(x'_{\infty} + \delta x, x^*_{\infty}) - \lambda(x'_{\infty} - \delta x, x^*_{\infty})}{2\Delta x}.$$
 (C.3)

We checked the integrations by running two independently constructed versions of the code. We also checked the eigenvalue measure of invasion fitness by direct measurement of the rate of increase of rare mutants.

⁸⁷⁶ D Fishing mortality under balanced harvest-⁸⁷⁷ ing

⁸⁷⁸ Balanced harvesting, as defined in this paper, sets the fishing mortality ⁸⁷⁹ rate on species *i* at time *t* in proportion to the current rate of somatic ⁸⁸⁰ production at each body mass *x*, from some mininum capture size x_{min} ⁸⁸¹ onwards. Production rate is measured as

$$p_i(x,t) = \epsilon_i(x) \ g_i(x,t) \ u_i(x,t) \ w_0 e^x,$$
 (D.1)

where $g_i(x,t)$ is the mass-specific assimilation rate of prey biomass Eq. (A.2), $\epsilon_i(x)$ is the proportion of this prey biomass allocated to somatic growth, $u_i(x,t)$ is the the density of individuals with log body mass in the range [x, x + dx], and $w_0 e^x$ is the predator mass. This gives a fishing mortality rate $F_i(x,t)$

$$F_i(x,t) = \begin{cases} 0 & \text{if } x < x_{min} \\ cp_i(x,t) & \text{if } x > = x_{min} \end{cases}.$$
 (D.2)

888

882

868

Here c is a constant of proportionality with dimensions vol. mass⁻¹ or area mass⁻¹, and can be thought of as a mass-specific exploitation ratio. Production rate changes over time as the density functions $u_i(x,t)$ change. Balanced harvesting tracks the changing production rate until the ecosystem reaches its ecological steady state. The calculations in this paper use the fishing mortalities at this steady state.