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1     Balanced exploitation and coexistence of interacting,  
2                     size-structured, fish species

3                     Richard Law, Michael J. Plank, Jeppe Kolding

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5     Alternative title: Coexistence of interacting fish species under balanced harvesting

6     Richard Law: York Centre for Complex Systems Analysis, Ron Cooke Hub, University of  
7     York, York YO10 5GE, UK

8     Michael J. Plank: School of Mathematics and Statistics, University of Canterbury, Christchurch,  
9     New Zealand

10    Jeppe Kolding: Department of Biology, University of Bergen, High Technology Center, P.O.  
11    Box 7800, N-5020 Bergen, Norway

12    Correspondence author: Richard Law: York Centre for Complex Systems Analysis, Ron  
13    Cooke Hub, University of York, York YO10 5GE UK. Tel +44 1904 325372; fax +44 1904  
14    500159; email: richard.law@york.ac.uk

15    Running title: balanced harvest and species coexistence

## Abstract

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This paper examines some effects of exploitation on a simple ecosystem containing two interacting fish species, with life histories similar to mackerel (*Scomber scombrus*) and cod (*Gadus morhua*), using a dynamic, size-spectrum model. Such models internalize body growth and mortality from predation, allowing bookkeeping of biomass at a detailed level of individual predation and growth, and enabling scaling up to the mass balance of the ecosystem. Exploitation set independently for each species with knife-edge, size-at-entry fishing, can lead to collapse of cod. Exploitation to achieve a fixed ratio of yield to productivity across species can also lead to collapse of cod. However, harvesting balanced to the overall productivity of species in the exploited ecosystem exerts a strong force countering such collapse. If balancing across species is applied to a fishery with knife-edge selection, size distributions are truncated, changing the structure of the system, and reducing its resilience to perturbations. If balancing is applied on the basis of productivity at each body size as well as across species, there is less disruption to size structure, resilience is increased, and substantially greater biomass yields are possible. We note an identity between the body size at which productivity is maximized and the age at which cohort biomass is maximized. In our numerical results based on detailed bookkeeping of biomass, cohort biomass reaches its maximum at body masses less than 1 g, unlike standard yield-per-recruit models, where body growth and mortality are independent externalities, and cohort biomass is maximized at larger body sizes.

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Keywords: balanced harvesting, ecosystem dynamics, productivity, resilience, size spectrum, yield-per-recruit

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# 1 Introduction

Conventional heavy exploitation of aquatic ecosystems generates major disruption. Effects on the ecosystems include truncation of age- and size-structures (Rice and Gislason, 1996; Hsieh et al., 2010), reduction in large-bodied species (Gu enette and Gascuel, 2012), destabilization of populations (Hsieh et al., 2010), discarding of unsuitable fish (Kelleher, 2005), and fisheries-induced evolution (Laugen et al., 2014). One obvious and incontestable response to this is to call for reduction in levels of exploitation. However, the importance of aquatic ecosystems to coastal and lake-margin communities around the world means that in many places human pressures on them are still likely to increase in the future.

Usually, the response to overfishing, collapsed stocks and fisheries-induced disruption is to try to improve the selectivity of fishing, to target more accurately the sizes and species needed for the market (COM, 2012). However, more careful targetting of large fish will disrupt size structure further, cause loss in resilience of stocks by reducing the abundance of large mature adults (Hsieh et al., 2010), and strengthen directional selection on life history traits potentially leading to faster fisheries-induced evolution. An alternative, motivated by ecological considerations, is to try to bring fishing closer in line with the natural productivity of components of aquatic ecosystems, the approach of so-called balanced harvesting (Zhou et al., 2010; Garcia et al., 2012). This is also selective, but there is an intuition that the overall effects of balanced harvesting should be less disruptive to the ecosystems themselves.

To go from an intuition about balanced harvesting to a firm foundation calls for quantitative analysis of exploitation patterns. Numerical analysis of balanced harvesting shows that it works well in preserving size structure, reducing the destabilizing effects of exploitation and, at the same time, increasing biomass yields, when applied to a single-species community living with a fixed plankton spectrum (Law et al., 2012, 2013). However, it is not clear how well it works in retaining a balance among species that live together and are coupled by body-size-dependent, predator-prey interactions. A recent study on generic behaviour of a multispecies community suggests the properties of preserving trophic structure and increasing biomass yields are retained (Jacobsen et al., 2014), but the detailed consequences of differ-

87 ent patterns of exploitation on the relative abundance and coexistence of interacting species  
88 are not known. In particular, the effect on coexistence of tuning fishing mortality species  
89 by species needs to be understood, as this is an important control measure for regulating  
90 multispecies aquatic ecosystems, such as those under the Convention for the Conservation of  
91 Antarctic Marine Living Resources (Miller and Slicer, 2014).

92 This paper examines how to organize exploitation of an aquatic ecosystem to maintain  
93 the balance of species, as well as to achieve sustainable yields from the species. As Jacobsen  
94 et al. (2014), we use dynamic size spectra, originally motivated by observed regularities in  
95 aggregated body size–abundance distributions of marine ecosystems (Sheldon and Parsons,  
96 1967; Sheldon et al., 1972; Platt and Denman, 1978; Silvert and Platt, 1978), and readily  
97 disaggregated to describe the changing size distributions of interacting taxa (Andersen and  
98 Beyer, 2006; Hartvig et al., 2011; Hartvig and Andersen, 2013). Size-spectrum dynamics  
99 explicitly track biomass as it moves through the ecosystem (Persson et al., 2014): fish only  
100 grow as a consequence of eating other organisms, and predation is an important cause of  
101 death. This flow of biomass is at the heart of balanced harvesting because the balancing is  
102 set by natural productivity, i.e. the flow of biomass through the system, per unit volume,  
103 per unit time.

104 We take the simplest possible setting of two interacting fish species in which to examine  
105 the effects of fishing on the balance between species, with parameters set to approximate the  
106 life histories of mackerel (*Scomber scombrus*, Scombridae) and cod (*Gadus morhua*, Gadidae).  
107 Mackerel abundance was high in the N E Atlantic in 2013 (possibly the highest level ever  
108 recorded), and its exploitation and interaction with other species is the subject of interna-  
109 tional debate. Thus knowledge on how it might interact with other commercially important  
110 species is of particular interest at the present time. However, the basic ideas in this paper  
111 would readily transfer to other ecosystems dominated by a small number of fish species, such  
112 as those in the Baltic Sea (Möllmann et al., 2008).

## 2 Unexploited ecosystem at equilibrium

We start by describing the dynamics of an unexploited ecosystem, as this provides a template onto which different kinds of exploitation can be imposed and compared.

To obtain dynamics similar to mackerel and cod, asymptotic body masses were assumed to be 650 g for mackerel, and 30 kg for cod, with an egg mass 0.001 g for both species. Mackerel has an important empirical property of growing from an egg to over 100 g in its first year (Villamor et al., 2004), which was achieved by assuming a relatively large volume searched per unit time, greater than that of cod (Hunter, 1981). In addition, the planktivorous behaviour of mackerel (Olaso et al., 2005) was incorporated by a relatively large preferred predator-prey mass ratio, compared to cod's, so that it feeds on smaller organisms. Parameters are summarized in Table 1, and information on sources is in Appendix B.

### 2.1 Model

A dynamic, size-spectrum model was used, as set out in Appendix A. Such models explicitly couple growth (somatic and gonadic) to predation mortality. When sexual maturity is reached, incoming biomass is allocated increasingly to reproduction, the proportion reaching 1 at the asymptotic body mass. We focus on behaviour close to the equilibrium of the ecosystem. Knowledge of the equilibrium properties is helpful, but it is important to bear in mind that this is not the only state that matters, and we envisage this study as giving a basis on which more complicated nonequilibrium and seasonal analyses could be built.

Mackerel and cod were treated as separate spectra, supported by a fixed plankton spectrum. (The plankton can be thought of as having a much shorter time scale for their dynamics: see Appendix A, Eq. (A.13).) For simplicity, feeding was assumed to be indiscriminate across taxa. This means that, in keeping with observations, there was cannibalism, as well as predation on other taxa (Smith and Reay, 1991; Neuenfeldt and Köster, 2000; Hillgruber and Kloppmann, 2001; Robert et al., 2008). Feeding was assumed to depend on the prey's body size relative to the predator's, for consistency with empirical information (Jennings et al.,

139 2001). Thus prey size increased smoothly as the fish grew, and an ontogenetic shift in the  
140 feeding niche lies at the heart of the model (Werner and Gilliam, 1984; Rudolf and Lafferty,  
141 2011). See Appendix A, Eq. (A.5) for the feeding-rate function.

142 Since cod grow larger than mackerel, the ecosystem might be thought of as a trophic chain  
143 in which cod feeds on mackerel. Such a construct is unwarranted: both species start at the  
144 same egg size, and small cod are a source of food for larger mackerel, as well as vice versa. In  
145 fact, mackerel were not able to persist under predation by cod in our model, when cod were  
146 excluded from their own diet. The two species do not separate cleanly into different trophic  
147 levels — to envisage the fish community as a simple food chain, would be to misconceive the  
148 way in which the ecosystem is organized.

## 149 **2.2 Equilibrium states**

150 With the parameters in Table 1, mackerel and cod coexisted at a stable equilibrium (leading  
151 real part of the eigenvalue of the Jacobian matrix:  $-0.17 \text{ y}^{-1}$ ). Note that dynamic size spectra  
152 have the feature of ‘distributed’ density-dependence, acting on body growth at all stages,  
153 as well as on mortality and reproduction. This greatly extends feedbacks (both positive  
154 and negative) beyond those assumed in standard stock-recruitment relations (Lorenzen and  
155 Enberg, 2002; Lorenzen, 2008), and beyond those in models that do not incorporate body  
156 growth. No stock-recruitment relation was imposed here (c.f. Jacobsen et al., 2014): all  
157 feedbacks acted internally through the size-dependent predation, and through the growth  
158 and reproduction that this feeding led to. This means that the relative abundances of the  
159 species were regulated directly by feeding and predation. It also avoided leakage of biomass  
160 from the ecosystem that would have had to be accounted for when examining mass flows  
161 (Section 2.6).

162 Both mackerel and cod also existed at stable equilibria in the absence of the other species  
163 (leading real parts of the eigenvalue of the Jacobians:  $-0.96, -0.44 \text{ y}^{-1}$  for mackerel and cod  
164 subsystems respectively). This is unsurprising in the case of mackerel, since food from the  
165 plankton spectrum is sufficient to enable growth to maturity. However, the single-species



166 equilibrium for cod is more delicate. Cod need a ‘trophic ladder’ (Hartvig and Andersen,  
167 2013) of smaller fish — they cannot get to maturity by consuming plankton alone. The  
168 trophic ladder could be supplied by mackerel or by small cod. Thus cod might establish itself  
169 in an ecosystem through a pre-existing population of mackerel. If mackerel was then wiped  
170 out for some reason, cod would remain in the ecosystem, mackerel only playing a catalytic  
171 role in community assembly (Law and Morton, 1996). Cod is vulnerable though: if its density  
172 for some reason was to fall sufficiently, growth to maturation through cannibalism would no  
173 longer be assured and renewal of the cod population would be threatened. This is an Allee  
174 effect (Hartvig and Andersen, 2013), as cod’s equilibrium at zero density is an attractor as  
175 well as the equilibrium at positive density, and is one of a number of ways in which an Allee  
176 effect can emerge from predator-prey interactions (de Roos et al., 2003; van Kooten et al.,  
177 2005).

### 178 **2.3 Departures from scale invariance**

179 In an idealized setting of scale invariance, the equilibrium size spectra would be straight lines  
180 on a log-log plot (Benoît and Rochet, 2004). However, explicit life histories inevitably break  
181 scale invariance of the species size spectra, leading to departures from linearity at the species  
182 level (Fig. 1). The equilibrium size spectra (Fig. 1 a,b) had bumps at body sizes around  
183 maturation, where incoming food is transferred increasingly to reproduction as opposed to  
184 somatic growth. Scale invariance was also broken by the fixed egg size.

185 Another consequence of breaking scale invariance was that mass-specific growth rates  
186 and productivities no longer decreased linearly in parallel on a log-log plot as functions of  
187 body mass (Fig. 1 c,d) (Law et al., 2013). Mass-specific growth rates were still monotonic  
188 decreasing, but productivities had intermediate maxima. This is important because the  
189 shape of the productivity function provides one basis for balanced harvesting (Law et al.,  
190 2012, 2013), and the shape of the function also gives some insight into yield-per-recruit (YPR)  
191 methods traditionally used in fisheries management (Section 3.3).

## 192 2.4 Productivity

193 Note that productivity of species  $i$  is defined here as an integral over body size  $x$  of the  
194 product of individual body mass, abundance, and mass-specific growth rate (dimensions: M  
195  $V^{-1} T^{-1}$ ). Since incoming mass is partitioned between somatic growth and reproduction, the  
196 productivity comes in two parts:

$$197 \quad \text{somatic: } P_i = \int \epsilon_i(x) g_i(x) u_i(x) w_0 e^x dx \quad (2.1)$$

$$198 \quad \text{reproductive: } R_i = \int (1 - \epsilon_i(x)) g_i(x) u_i(x) w_0 e^x dx, \quad (2.2)$$

199 where  $w_0$  is an arbitrary mass to scale from mass to log mass ( $x = \log(w/w_0)$ ),  $u_i(x)$  de-  
200 notes the density of species  $i$  at body size  $x$ , and  $g_i(x)$  is the mass-specific growth rate, of  
201 which a proportion  $\epsilon_i(x)$  is channelled into somatic material and a proportion  $1 - \epsilon_i(x)$  into  
202 reproduction.

## 203 2.5 Growth trajectories

204 The average growth trajectories from the model at equilibrium emerged simply as a result  
205 of feeding and growth, without imposing any explicit functional form (Fig. 1 e,f). Their  
206 resemblance to estimated von Bertalanffy growth functions for mackerel and cod (Villamor  
207 et al., 2004; Limburg et al., 2008) is expected, because we used reported functions to find  
208 appropriate volumes searched per unit time in the model. Nonetheless, the trajectory for  
209 mackerel captures properly its remarkably fast growth over its first year of life and its much  
210 slower growth subsequently, which the fitted von Bertalanffy function does not. Note that  
211 growth of cod benefits from the presence of mackerel.

212 **2.6 Mass balance**

213 At equilibrium, certain mass balances must be satisfied. The basic equality is that all mass  
 214 losses from each species  $i$  must be balanced by corresponding gains (Balance 1):

215 
$$P_i + R_i = D_i + D_{o,i} + Y_i + R_i/2, \quad (2.3)$$

216 with dimensions:  $M V^{-1} T^{-1}$  throughout (derived from integrals over body size at equilibrium  
 217 in Appendix C).  $P_i$  is the productivity from somatic growth (Eq. 2.1),  $R_i$  is the productivity  
 218 from mass flow to reproduction (Eq. 2.2),  $D_i$  is mass loss through predation,  $D_{o,i}$  is the mass  
 219 loss through natural mortality other than predation, and  $Y_i$  is mass loss due to fishing (used  
 220 in the next section). The extra loss term  $R_i/2$  comes from assuming that half the mass to  
 221 reproduction is channelled through males, and that this is also lost.

222 Separate from Balance 1, all gains to the fish community from the plankton must be  
 223 balanced at equilibrium by corresponding losses from the fish community. This gives Balance  
 224 2:

225 
$$\sum_{i=1}^n (P_{i0} + R_{i0}) = \sum_{i=1}^n \left( (1 - K) \sum_{j=1}^n D_{ji} + D_{o,i} + Y_i + R_i/2 \right), \quad (2.4)$$

226 where  $P_{i0}, R_{i0}$  are the productivity inputs to  $i$  from plankton,  $K$  is the food conversion  
 227 efficiency (Table 1),  $D_{ji}$  is the mass loss to  $i$  from predation by  $j$ , and  $n$  is the number of  
 228 fish species. Summing Balance 1 over all fish species and subtracting Balance 2 leaves a  
 229 remaining balance that comes from recycling mass among fish. This is Balance 3:

230 
$$\sum_{i=1}^n \sum_{j=1}^n (P_{ij} + R_{ij}) = K \sum_{i=1}^n \sum_{j=1}^n D_{ji}. \quad (2.5)$$

231 Further disaggregation of Balance 3 to pairwise interactions between species is not possible  
 232 because, in general, interactions between species are not symmetric; for instance, one species  
 233 might only be the prey of the other.

234 In the mackerel-cod system, the rate of mass flow from cod to mackerel was similar to the  
 235 rate from mackerel to cod, at equilibrium (Fig. 2). Mackerel is as important a predator on

236 cod, as cod is on mackerel, which illustrates how misleading it is to think of these species  
237 as forming a trophic chain. However, mass flow through cannibalism was much greater  
238 in mackerel than in cod, because of the greater abundance of mackerel over the body-size  
239 range it feeds on (Fig. 1a,b). This means that the efficiency with which mackerel turns its  
240 production into cod food, its ecotrophic efficiency (Dickie, 1972), is rather low:  $0.94/4.74 =$   
241  $0.20$ . Cod, with relatively little cannibalism, was more efficient at turning production into  
242 mackerel food:  $0.78/0.94 = 0.83$ . The transfer efficiency is the product of the ecotrophic  
243 efficiency and the food conversion efficiency (Dickie, 1972). Thus, with a food conversion  
244 efficiency  $K = 0.2$  for both species (Table 1), cannibalism makes the transfer efficiency of  
245 turning mackerel biomass into cod biomass low ( $0.04$ ), compared with that of turning cod  
246 biomass into mackerel ( $0.17$ ). Balances (1), (2) and (3) (Eqns (2.3), (2.4), (2.5) respectively),  
247 were close to zero in both species, but not exact, because of the discretization needed to do  
248 the computation.

### 249 **3 Exploiting the ecosystem**

250 We examine harvesting at equilibrium, beginning with conventional, single-species manage-  
251 ment, where size-at-entry regulations are applied one species at a time, ignoring biological  
252 predator-prey interactions across species. From this starting point, we make two steps to-  
253 wards an ecosystem approach. The first is to find a balance across species that promotes their  
254 coexistence as fishing mortality increases, without taking into account the size-dependence  
255 of productivity. This is not a big step to make, as it is a matter of how to tune fishing  
256 mortality rates across species using whatever distribution of fishing over body size is already  
257 in place. The second step involves balancing across body size as well as across species. This  
258 is more demanding, but it should be considered because productivity changes greatly as fish  
259 get larger (see for instance Fig. 1 c,d).

260 These comparisons complement those made by Jacobsen et al. (2014). Their unbalanced  
261 harvesting patterns used a fixed fishing mortality rate for every species, whereas the single-  
262 species management here was designed to show some consequences of applying different

263 fishing mortalities that do not simultaneously allow for interactions between the species.  
264 Their balanced harvesting patterns were based on fixed, external, scaling assumptions about  
265 productivity, whereas here fishing was continually adjusted across species on the basis of  
266 information about productivity emerging from the current pattern of harvesting, until equi-  
267 librium was reached.

### 268 **3.1 Single-species management**

269 Here entry into the fishery was assumed to be knife-edged, starting at 100 g for mackerel  
270 and at 1000 g for cod, fishing mortality being the same at all larger body sizes. The fishing  
271 mortality rate was fixed for one species and altered for the other species, in keeping with a  
272 management regime focused on single species. In view of the high productivity of mackerel,  
273 the greatest sustainable biomass yield overall would be expected from eliminating cod. But  
274 we do not go into this, as it would not be in the spirit of conservation of the ecosystem.  
275 A maximum sustainable yield for a species is clearly contingent on the abundance of other  
276 species (its predators and prey), and cannot be decided in isolation.

277 The significant feature of the results (Fig. 3) is not the change in stock biomass and yield  
278 of the species in which fishing mortality is varied; rather it is the change in the species in  
279 which fishing mortality is fixed. Thus, in Fig. 3a, where fishing on cod was fixed at  $F_c = 0.5$   
280  $y^{-1}$ , the cod biomass and yield were zero when fishing on mackerel was relatively light, as  
281 cod could not maintain a population under the combined adverse effects of mortality from  
282 harvesting and heavy predation from a large population of mackerel. The combination of  
283 abundant mackerel and heavy fishing on cod is evidently problematic for continued existence  
284 of cod. The biomass of mackerel decreased as it was fished harder, leading to less predation by  
285 mackerel on cod, and an increase in yield of cod. A benefit to cod of this kind has been noted  
286 following the collapse of herring stocks in the North Sea (Speirs et al., 2010); see also van  
287 Denderen and van Kooten (2013). For large enough  $F_m$ , however, the yield of cod started to  
288 decline again, because mackerel's other role as a source of food for large cod was jeopardized.  
289 This happened despite a continuing increase in biomass of cod, because smaller cod benefited  
290 from reduced predation by mackerel. To put it another way, cod's size spectrum responded

291 to the loss of mackerel in different ways at different body sizes.

292 In the reverse case (Fig. 3b), where fishing on mackerel was fixed at  $F_m = 1.0 \text{ y}^{-1}$ , the  
293 mackerel yield increased monotonically with heavier fishing on cod, through the reduction of  
294 predation by cod on mackerel, until cod collapsed at about  $F_c = 0.8 \text{ y}^{-1}$ . A similar effect of  
295 increasing  $F_c$  has been noted on sprat and herring in a recent multispecies assessment of the  
296 Baltic Sea (ICES, 2013c).

297 As is well understood in fisheries science (ICES, 2013b), it is difficult to manage a fishery  
298 at the ecosystem level by controlling fishing one species at a time, when species are coupled  
299 through predation. The effect of coupling is particularly obvious when the number of species  
300 is small. Increasing the number of species would dilute this effect, as would a reduction in  
301 the strength of coupling between the species.

### 302 **3.2 Harvest balanced across species, not body size**

303 An alternative to the single-species approach is to try to achieve a balance in fishing across  
304 species. ‘Balancing’ could be interpreted in a number of different ways – there is no gen-  
305 eral agreement on this (see Section 5). In any event, balancing across species can be done  
306 regardless of the way in which fishing is distributed over body sizes within species. So we  
307 continue with the size-at-entry fishery on mackerel and cod in Section 3.1, but instead of  
308 managing each species in isolation, we adjust fishing mortality to try to achieve a balance  
309 between them. There are many methods for doing this (Section 5), of which we investigate  
310 two here.

311 The first approach is to adjust the fishing mortality on each species to try to get a similar  
312 ratio  $Y_i/P_i$  of yield to productivity for each species. This was achieved by setting the fishing  
313 mortality according to  $F_i = c_1 P_i/B_i^*$  (Appendix D, Eq. (D.3)), where  $c_1$  is a dimensionless  
314 constant describing the overall intensity of fishing and  $B_i^*$  is the amount of biomass of species  
315  $i$  in the fishery (i.e. individuals with body size greater than the size-at-entry). In this way, a  
316 small yield is taken from a species with low productivity and a large yield from one with high  
317 productivity. Fig. 4a shows  $Y$  against  $P$ , for each species, as the overall fishing intensity

318  $c_1$  is gradually increased. Because this fishing pattern guarantees that  $Y_i/P_i = c_1$  for each  
319 species, the pairs of points in Fig. 4a lie on parallel lines of constant  $Y/P$ , moving up the  
320 graph as  $c_1$  increases. However, the figure shows that, while the exploitation ratios  $Y_i/P_i$   
321 were balanced across species, the productivities were not. As the fishing intensity increased,  
322 the productivity of mackerel increased slightly, while the productivity of cod crashed as the  
323 cod population collapsed.

324 A second, alternative approach, is simply to set fishing mortality in direct proportion to  
325 the productivity of the species, i.e.  $F_i = c_2 P_i$  (Appendix D, Eq. (D.4)), where  $c_2$  is a constant  
326 describing the overall intensity of fishing, in this case with dimensions  $V M^{-1}$  (Fig. 4b). This  
327 time, the pairs of points in Fig. 4b do not lie on parallel lines because the species no longer  
328 have the same exploitation ratios  $Y_i/P_i$  (the exploitation ratio for mackerel is roughly three  
329 times that of cod). Importantly, adjusting the fishing mortalities in tune with the current  
330 productivities kept the two species much better in balance up to levels of exploitation that  
331 would have caused collapse of cod in Fig. 4a.

### 332 **3.3 Harvest balanced across species and body size**

333 Fisheries that concentrate on large body sizes miss a substantial part of the productivity of  
334 aquatic ecosystems (Law et al., 2012, 2013). Here, we extend the approach in Section 3.2 to  
335 examine the effects of harvesting balanced by body size, as well as by species. A minimum  
336 body size for exploitation is still needed, and we set this at 1 g.

337 In doing this, we point out the following formal connection between (a) harvesting by size-  
338 dependent productivity, and (b) harvesting to maximize YPR within cohorts of individuals.  
339 For a species at equilibrium, there can exist one (or more) body size  $x^*$  with the following  
340 three properties: (a) it gives a maximum productivity with respect to body size  $x$ ; (b) it gives  
341 a maximum biomass for a cohort with respect to age; (c) it achieves equality between the  
342 mass-specific growth rate and total death rate (Hillis and Arnason, 1995; Houde, 1997). (See  
343 Appendix E for an explanation.) Hence, the messages from YPR models and from balanced  
344 harvesting are actually quite similar. YPR sets fishing to start near the biomass peak of the

345 cohort, and equivalently, balanced harvesting sets fishing to be greatest at the productivity  
 346 peak, which occurs at the same age and body size. The key difference between  $x^*$  from  
 347 biomass bookkeeping in size-spectra models, and  $x^*$  from standard YPR models with growth  
 348 uncoupled from mortality, is numeric: in the example in this paper for instance,  $x^*$  occurs at  
 349 body sizes  $< 1$  g (see Section 5).

350 As in Section 3.2, in the absence of agreement as to what exactly it means to balance  
 351 exploited species, we consider two of many possible options. The first makes fishing mortality  
 352 proportional to the mass-specific, somatic growth rate of individuals of species  $i$  and body  
 353 size  $x$ , i.e.  $\mu_{f,i}(x) = c\epsilon_i(x)g_i(x)$  (Appendix D, Eq. (D.5)), where  $c$  is a dimensionless  
 354 constant describing the overall intensity of fishing (Fig. 5). This is consistent with the  
 355 notion of productivity suggested for balanced harvesting in Note 8 of Garcia et al. (2012), at  
 356 least so far as dimensions are concerned. Balancing now applies across species and at every  
 357 harvested body size because, at equilibrium, the exploitation rate is scaled throughout by  
 358 the same value  $c$ . The outcome is that the species have the same ratio  $Y_i/P_i^*$ , where  $P_i^*$  is the  
 359 productivity in the harvested size range. For comparability with the other figures we use  $P_i$ ,  
 360 the productivity over all body sizes, so in fact the pairs of points in Fig. 5a lie approximately,  
 361 but not exactly, on parallel lines. However, as in Fig. 4a, cod collapsed as the overall fishing  
 362 intensity increased, and the productivity of mackerel increased as this happened (Fig. 5a).  
 363 At the point of elimination of cod, the ecosystem productivity was close to 120 % of its  
 364 virgin value, because the inefficient transfer of biomass to cod was removed, and mackerel  
 365 was being harvested at less than 50 % of its single-species MSY level. Hence, setting fishing  
 366 in proportion to the mass-specific, somatic growth rate does not maintain a desirable balance  
 367 of species.

368 A second, alternative approach is to set fishing in proportion to productivity at every body  
 369 size in both species, as defined in terms inside the integral of Eq. (2.1), i.e.  $\mu_{f,i}(x) = cp_i(x)$ ,  
 370 where  $c$  is a constant describing the overall intensity of harvesting with dimensions  $V M^{-1}$ ,  
 371 and  $p_i(x)$  is the productivity of species  $i$  at body size  $x$  (Fig. 5b) (Appendix D, Eq. (D.7)).  
 372 This exploitation pattern held the species in balance better than exploitation in proportion to  
 373 the mass-specific growth rate (compare with Fig. 5a). Pairs of points corresponding to each



374 fishing intensity  $c$  do not lie on lines of constant  $Y/P$ , and low levels of fishing in particular  
375 show greater  $Y_i/P_i$  ratios emerging for mackerel than for cod. The species coexisted until  
376 exploitation brought the total ecosystem productivity down to about 30 % of its virgin value.  
377 The yields were also substantially greater than those in Fig. 4b, as the high productivity at  
378 small body sizes was better exploited.

## 379 4 Conservation and sustainable exploitation

380 Harvesting exerts a strong force countering the loss of species under exploitation, when set  
381 in balance with the overall productivity of each species in the exploited ecosystem. The per  
382 capita fishing rate rises as productivity increases so that a single species does not come to  
383 dominate the system, and it falls as productivity decreases so that rare species are protected.  
384 It acts as a form of intraspecific, density-dependent mortality that introduces a negative  
385 feedback. This diversity-maintaining effect of balanced harvesting can be seen in Fig. 4b and  
386 5b.

387 Effects on the shape of species size spectra are more intricate, because fishing has indirect,  
388 as well as direct, effects on the spectra. To illustrate this, Fig. 6 compares the spectra from  
389 the contrasting patterns of fishing in Section 3, after the total biomass at equilibrium has  
390 been brought down to approximately 0.75 of its unharvested value. (Cod was absent at this  
391 biomass in Fig. 4a, 5a, and it is coincidental as to whether there is coexistence for a given  
392  $F_m, F_c$  pair in a standard, size-at-entry fishery, so we consider only the fishing patterns in  
393 Fig. 4b, 5b.) As expected, there was truncation of the size structure in the size-at-entry  
394 fishery with balancing across species (Fig. 6a), because such fishing was still focused on large  
395 individuals. However there was also some truncation in the cod spectrum when balancing  
396 was across body size as well as species (Fig. 6b), though less than in Fig. 6a. This was an  
397 indirect consequence, rather than a direct effect of fishing mortality, because fishing reduced  
398 the food available for large cod, and they grew more slowly. Notice that, despite the fact  
399 that cod was generating yield, its abundance rose above its unexploited level, as a result of  
400 the strong equalizing force of balanced harvesting.

401 Truncation of age structure in size-at-entry fisheries destabilizes the mackerel-cod ecosys-  
402 tem, just as it is known to do in single-species analyses (Law et al., 2012): coupling the  
403 dynamics of two species does not remove the instability (Fig. 7). This figure includes a  
404 conventional size-at-entry fishery, with fishing mortality on mackerel twice that on cod, these  
405 mortalities being increased proportionately up to a value at which cod was eliminated. The  
406 real part of the leading eigenvalue (a measure of instability) increased as fishing was made  
407 more intense, eventually becoming positive and destabilizing the ecosystem. A similar change  
408 was evident when exploiting a size-at-entry fishery with balancing across species. It was only  
409 under full balancing across body size as well as species that the system remained resilient,  
410 the eigenvalue becoming more negative until fishing mortality was large. We interpret this  
411 difference as an outcome of more big old fish being present under full balanced harvesting,  
412 spreading reproduction over a longer adult life.

413 Consistent with the maintenance of a greater stock of big old fish are the tails of the  
414 survivorship curves of cohorts in Fig. 8. Although the size spectrum of cod was truncated  
415 under full balancing (Fig. 6b), evidently this was because cod grew more slowly, not because  
416 old fish were absent. It is notable how much closer to the unexploited ecosystem the survivor-  
417 ships were when fishing was balanced across body size as well as species. This implies that  
418 fishing mortality was to some extent replacing natural mortality, rather than adding to it  
419 (Law et al., 2013). Harvesting some large fish releases their prey from predation; these prey  
420 are then available for harvesting, as are their prey, and so on. When balanced across body  
421 size, harvesting evidently keeps the combined mortality from fishing + predation relatively  
422 close to predation mortality in the absence of fishing. Such replacement may underly the  
423 relatively benign effects of exploitation, when in balance with productivity at body size and  
424 across species.

## 425 5 Discussion

426 Our results demonstrate that harvesting, when held in balance with productivity, is poten-  
427 tially a strong force preventing collapse of exploited species. This applies both when effects

428 of body size are ignored and when effects of body size are taken into account. Note that the  
429 term ‘productivity’ follows its normal usage in ecosystem ecology as a mass per unit volume  
430 (area) per unit time, i.e. with dimensions  $M V^{-1} T^{-1}$  (see of Eq. (2.1)), rather than a mass-  
431 specific rate (dimensions:  $T^{-1}$ ) (Garcia et al., 2012). The amount of mass in the species  
432 matters as much as the per-unit-mass rate at which it is increasing when setting fishing mor-  
433 tality. Importantly, productivity was measured at the time of harvesting, so fishing mortality  
434 tracked and responded to the current productivity of exploited species. This is in contrast  
435 to previous work which drew on external information either about an unharvested ecosystem  
436 (Law et al., 2012, 2013), or an external scaling law (Jacobsen et al., 2014). Adaptive fishing  
437 of the kind used here calls for information on how fast fish are growing, readily available  
438 from size-at-age data, and stock abundance (available from fishery surveys, and catch per  
439 unit effort), disaggregated to the appropriate level.

440 There is no generally accepted notion of what it means to achieve a balance between  
441 species under exploitation. We tested a few of the many possibilities, and do not claim to  
442 have found the best answer. For instance, one could maintain the same ratio for biomasses  
443 or productivities of the species as in an unexploited system. However, productivity is a  
444 natural choice where exploitation of an ecosystem is concerned, and is at the heart of current  
445 discussions about balanced harvesting. Note that the size spectra of mackerel and cod were  
446 pulled towards each other under full balancing across body size and species (Fig. 6), making  
447 the species more even; in fact balanced harvesting made cod more abundant than it would  
448 have been in the absence of exploitation. We conjecture that full balancing by productivity  
449 has the potential to increase biodiversity above that of an unexploited ecosystem; this could  
450 be seen as interference with its natural structure. Other results from body-size balancing  
451 remain broadly similar to those observed previously (Law et al., 2012, 2013; Jacobsen et al.,  
452 2014), namely, generating greater biomass yields, increased system resilience, and enabling  
453 more substitution of natural mortality by fishing mortality.

454 A feature of balancing by productivity was an emergent exploitation ratio  $Y_i/P_i$  for mack-  
455 erel greater than that for cod. We interpret this as an outcome of mackerel’s especially rapid  
456 growth when small. It has been suggested that, in a simple food chain, exploitation rates on

457 intermediate species should be lower than on top species, so that some part of the biomass  
458 of intermediate species is kept in place to support species higher up the food chain (Kold-  
459 ing, 1993). However, as trophic levels become blurred through cannibalism and reciprocal  
460 predation, it seems that a greater exploitation rate is needed on the smaller, more produc-  
461 tive species. Otherwise the abundant smaller species (here mackerel) drives down the larger  
462 species (here cod) by heavy predation, and this is deleterious to the yield from the larger  
463 species. It should be kept in mind though, that this could be context specific, being caused  
464 here by mackerel's especially fast somatic growth in its first year.

465 Fisheries science has a rule of thumb of setting fishing mortality of different species in  
466 proportion to their natural mortalities. However natural mortality is a moving target, because  
467 it depends on fishing mortality: for instance, heavier exploitation reduces stock density, which  
468 reduces cannibalism and predation on other species. It also leaves open the question as to  
469 what natural mortality should be used, as this mortality varies greatly across age and body  
470 size. An aggregate measure of natural mortality based on a ratio of productivity to biomass  
471 might be used, to which fishing mortality could be matched (as in Figure 4a), but this would  
472 not promote coexistence of exploited species according to our results.

473 The formal equivalence of the body size maximizing (a) productivity and (b) cohort  
474 biomass, bring together balanced-harvesting and conventional YPR approaches. In doing  
475 this, a remarkable divergence emerges from the calculations. On one hand, our calculations  
476 on mackerel and cod give maximum productivities at body masses less than 1 g. On the other  
477 hand, minimum legal landing sizes of these species in the European Union, underpinned by  
478 a number of factors including cohort biomass, are currently 20 to 30 cm for mackerel, and 30  
479 to 35 cm for cod. This points to an important lack of understanding as to how mass flows  
480 through marine ecosystems. We illustrate the problem in Fig. 9, in which cohort biomass  
481 emerging from our unexploited equilibrium ecosystem is plotted with the mass-specific growth  
482 rate and total death rate. As expected from the productivities with their maxima at body  
483 sizes less than 1 g (Fig. 1c,d), maximum cohort biomasses (where the rate curves first inter-  
484 sect) occur shortly after egg hatching. In the case of cod there is a second small maximum  
485 at about age 4 y, as there are two further intersections of its rate functions. (We have not

486 dealt with an intersection at the very early larval stage (Houde, 1997), but would not expect  
487 this to have major effect on subsequent behaviour.) Notice that, if the natural death rate  
488 is not known and is replaced by an arbitrary value, say  $1 \text{ y}^{-1}$ , the intersection occurs at an  
489 age greater than 1 y, leading to the prediction that cohort biomass would not be maximized  
490 until the fish are considerably older. In doing this, however, the much higher mortality rate  
491 of fish within the first year is not being taken into account.

492 Obviously there are assumptions built into the feeding behaviour of fish in our model.  
493 However, we have done the mass balancing in more detail than previous work, starting  
494 with individual growth, and working through population dynamics, up to the ecosystem  
495 level (Persson et al., 2014). Among the other main multispecies approaches (Plagányi, 2007),  
496 ATLANTIS comes nearest to doing this (Horne et al., 2010), but, with disaggregation of prey  
497 already taken down to species, it does not deal with additional complications of mass flow  
498 from continuous body-size distributions of prey into the growth of predators. ECOSIM does  
499 biomass balancing, but aggregates over body size, often focusing on adults of species, prior  
500 to computation of mass flows, and does not deal with the continuous growth of organisms  
501 (Walters et al., 1997). OSMOSE disaggregates species by age, and uses an external function  
502 for body growth, modified by food availability (Shin and Cury, 2004). Gadget disaggregates  
503 by species, body size and area, and uses external information on body growth (Begley and  
504 Howell, 2004). The ecosystem approach adopted by ICES in the North Sea (ICES, 2013b)  
505 estimates the size-dependent predation mortality across species from a stochastic multispecies  
506 size-dependent food selection model (SMS) (Lewy and Vinther, 2004) but does not deal with  
507 the consequences for body growth. The challenge the standard YPR calculation faces is to  
508 find enough food in the ecosystem to achieve the observed growth of fish without increasing  
509 natural mortality; otherwise the body size at which cohort biomass is maximized will typically  
510 become smaller when mortality is accounted for. This needs investigation.

511 As Jacobsen et al. (2014) point out, the economic value of small fish is low in major com-  
512 mercial fisheries. However, size structures and resilience are being damaged in the ecosystems  
513 that support these fisheries (Rice and Gislason, 1996; Hsieh et al., 2010), and strong direc-  
514 tional selection on genetic variation in life-history traits is being generated (Sharpe and

515 Hendry, 2009). Conservation calls for a change in approach, as does an ecosystem approach  
516 under the code of conduct of responsible fisheries (Garcia and Cochrane, 2005), even if eco-  
517 nomics do not. In addition, economic arguments for not catching small fish do not apply to  
518 the small-scale fisheries that employ most of the World’s fishers (Mills et al., 2011; Kolding  
519 et al., 2014). It is a matter of particular concern that exploitation of small fish is actively  
520 discouraged in parts of the developing world where there is serious poverty, because of a man-  
521 agement agenda from the developed world focused on harvesting large fish (Kolding and van  
522 Zwieten, 2011). Both food production and conservation stand to benefit from more balanced  
523 harvesting across body sizes, according to the results emerging from size-spectra models.

524 We make no claim that harvesting, when balanced by productivity across body size and  
525 species, is a general answer to the exploitation of aquatic ecosystems. But our numerical re-  
526 sults suggest it does have several useful properties. Fishing, when set to current productivity  
527 of species, is a powerful force promoting species coexistence. In addition, fishing when set to  
528 productivity across body size, allows biomass yields to be increased, truncation of size and  
529 age structure to be reduced, and resilience of aquatic ecosystems to be increased.

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Table 1: Model parameters and values.

Parameter	mackerel	cod	Unit	Comments
<i>Fish life histories:</i>				
$w_0e^{x_{i,0}}$	0.001	0.001	g	mass of fish egg
$w_0e^{x_{i,m}}$	200	2000	g	mass at 50% maturity
$w_0e^{x_{i,\infty}}$	650	30000	g	asymptotic mass
$\rho_{i,m}$	15	8	–	controls the body-size range over which maturation occurs
$\rho$	0.2	0.2	–	exponent for approach to asymptotic body size in reproduction function
<i>Dynamic size spectra of fish species:</i>				
$K$	0.2	0.2	–	food conversion efficiency
$\alpha_i$	0.8	0.8	–	search rate scaling exponent
$A_i$	750	700	$\text{m}^3 \text{y}^{-1} \text{g}^{-\alpha}$	feeding rate constant
$\beta_i$	6	4.5	–	natural log of mean predator prey mass ratio
$\sigma_i$	2.5	1.9	–	diet breadth
$\theta_{i,0}, \theta_{i,1}, \theta_{i,2}$	1	1	–	predator preferences for prey types 0, 1, 2
$\mu_{o,i}^{(0)}$	0.1	0.1	$\text{y}^{-1}$	intrinsic (non-predation) mortality rate at birth
$\xi$	-0.15	-0.15	–	exponent for intrinsic (non-predation) mortality
<i>Fixed plankton size spectrum:</i>				
$w_0e^{x_{0,min}}$	$4.8 \times 10^{-11}$		g	lowest body mass of plankton
$w_0e^{x_{0,max}}$	0.03		g	greatest body mass of plankton
$u_{0,0}$	100		$\text{m}^{-3}$	plankton density at 1 mg
$\gamma$	2		–	exponent of plankton spectrum

## 725 **Figure legends**

726 Figure 1: Equilibrium properties of an unexploited ecosystem, with parameters as in Table  
727 1. Heavy lines are for coexisting mackerel and cod; thin lines are for systems with a single  
728 species. Continuous lines refer to the left-hand vertical axes, and dashed lines to the right-  
729 hand axes. The dotted lines in (e) and (f) are von Bertalanffy growth curves for mackerel  
730 (Villamor et al., 2004) and cod (Limburg et al., 2008).

731 Figure 2: Mass flows at equilibrium for the unexploited ecosystem in Fig. 1 (units:  $\text{g m}^{-3}$   
732  $\text{y}^{-1}$ ). The calculation was done without the diffusion term of the dynamical system, with  
733  $dx = 0.025$ . See Eq. (2.3) *et seq.* for notation.

734 Figure 3: Equilibrium biomasses (thick lines) and yields (thin lines) in fisheries with fishing  
735 mortality  $F$  fixed for one species, and variable for the other. Continuous lines: mackerel;  
736 dashed lines: cod. Fishing mortality rates are: (a) variable mackerel  $F_m$ , fixed cod  $F_c = 0.5$   
737  $\text{y}^{-1}$ ; (b) variable cod  $F_c$ , fixed mackerel  $F_m = 1.0 \text{ y}^{-1}$ . Other parameters as in Table 1.

738 Figure 4: Equilibrium yields in a size-at-entry fishery with balancing between species; mack-  
739 erel: filled circles; cod: open circles. Dashed lines are lines of constant exploitation rate: 0.01,  
740 0.02, 0.04, 0.06, 0.08, 0.1, 0.5, 1.0, with exploitation rate increasing moving up the figures.  
741 (a) Fishing mortality retaining the same ratio  $Y_i/P_i$  in each species, up to collapse of cod.  
742 (b) Fishing mortality set in proportion to productivity  $P_i$  of each species. Other parameters  
743 as in Table 1.

744 Figure 5: Equilibrium yields with balancing across species and over body sizes within species;  
745 mackerel: filled circles; cod: open circles. Dashed lines are lines of constant exploitation  
746 rate: 0.01, 0.05, 0.1, 0.5, 1.0, with exploitation rate increasing moving up the figures. (a)  
747 Fishing mortality balanced by mass-specific growth rate,  $g_i(x)$  of each species and each body  
748 size within species, and increased up to collapse of cod. (b) Fishing mortality balanced by  
749 productivity of each species and each body size within species. Other parameters as in Table  
750 1.

751 Figure 6: Equilibrium size spectra of mackerel (dotted) and cod (continuous) under contrast-  
752 ing patterns of harvesting (heavy) and in the absence of exploitation (light). Total biomass



753 (mackerel+cod) at harvested equilibria is approximately 0.75 of the unexploited ecosystem.  
754 (a) Balancing across species in a size-at-entry fishery (Fig. 4b);  $F_m = 2.17$ ,  $F_c = 0.66 \text{ y}^{-1}$ . (b)  
755 Balancing across body size and species (Fig. 5b); constant  $c_4$  that weights the productivity  
756 at each body size for generating size-specific fishing rates is  $7.0 \text{ m}^3 \text{ g}^{-1}$ . Other parameters as  
757 in Table 1.

758 Figure 7: Stability of exploited ecosystems at equilibrium under contrasting patterns of  
759 harvesting. Conventional size-at-age fishery (continuous), size-at-entry with balancing across  
760 species (dashed), balancing across body size and species (dotted). Fishing mortalities defined  
761 in the text; other parameters as in Table 1. The upper two lines are terminated at the point  
762 where cod was eliminated; mackerel and cod coexisted over the full range of fishing in the  
763 lowest line.  $Y_i/B_i$  gives a comparable measure of the average fishing mortality for different  
764 kinds of harvesting. The real part of the leading eigenvalue  $\lambda$  measures the time course  
765 of small perturbations from equilibrium, the return to equilibrium becoming slower as the  
766 eigenvalue approaches zero from a negative value, and not returning at all when positive.

767 Figure 8: Survivorships computed under the conditions of Fig. 6, for (a) mackerel, and (b)  
768 cod. Survivorships in unexploited ecosystem (continuous), size-at entry fishery with balancing  
769 across species (dashed), full balancing across body size and species (dotted). Parameter values  
770 as in Fig. 6.

771 Figure 9: Cohort biomass (heavy lines) in the equilibrium, unexploited ecosystem in Fig. 1  
772 for: (a) mackerel, (b) cod, computed as the product of body mass and proportion surviving  
773 from age 0 to each age. The somatic growth rates (dotted lines) and total death rates (dashed  
774 lines) are included to show that extrema of cohort biomasses occur at the intersections of the  
775 rate lines. Note the resemblance of these cohort biomasses to the productivities in Fig. 1c,  
776 d.

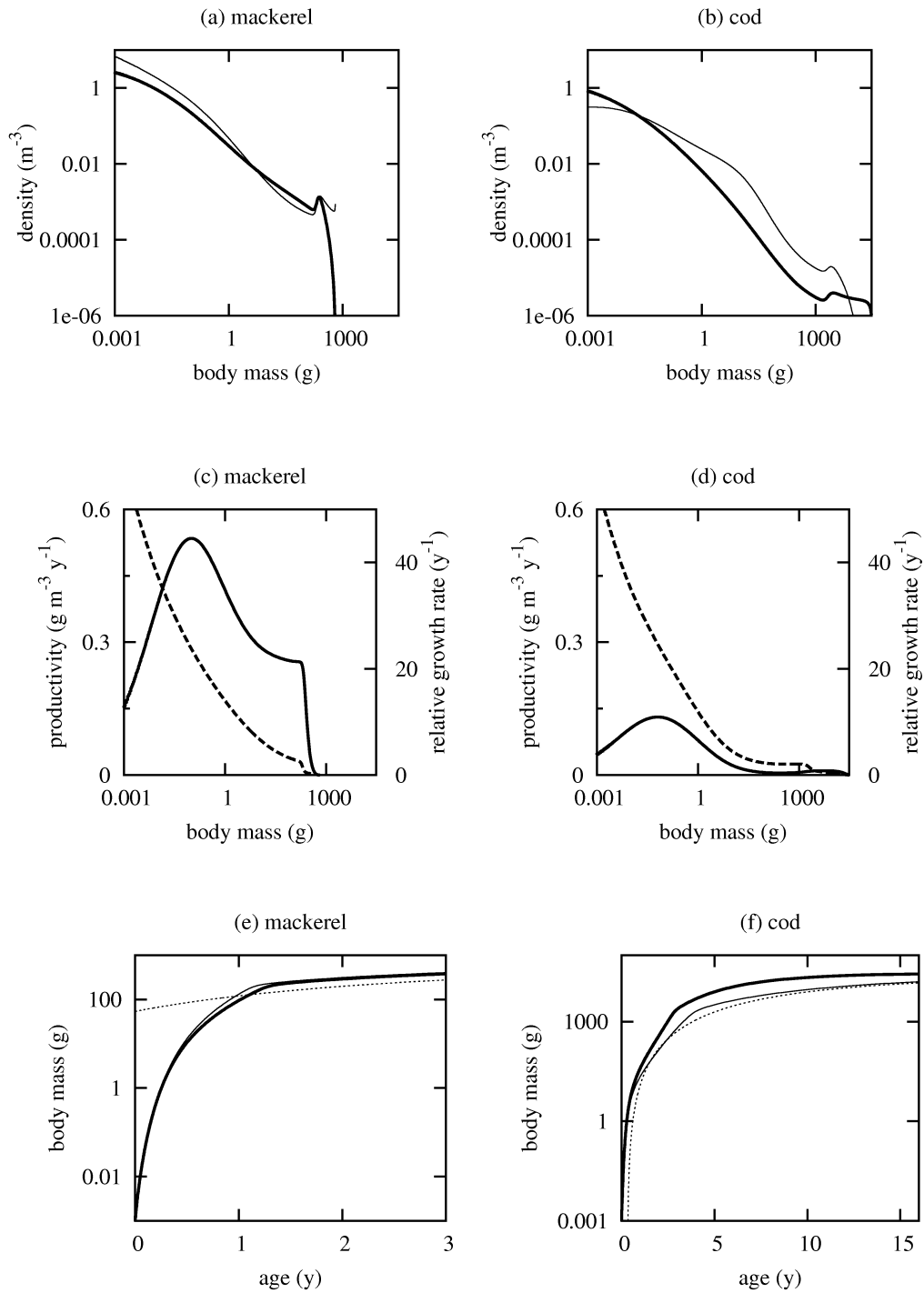


Figure 1:



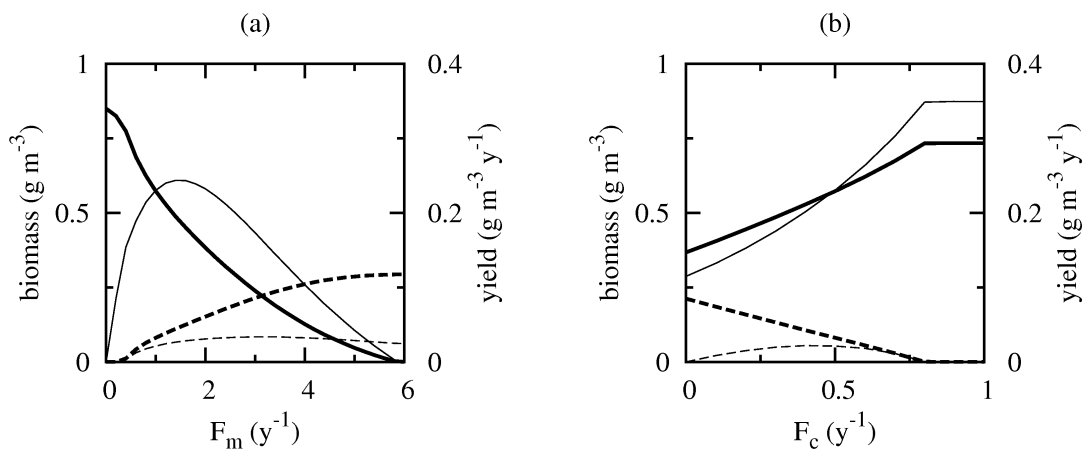


Figure 3:

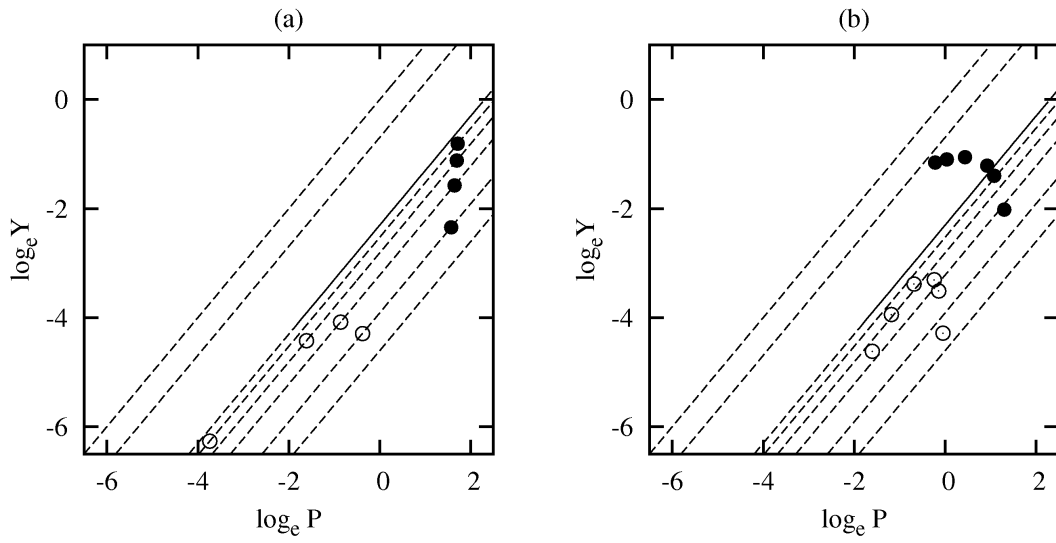


Figure 4:

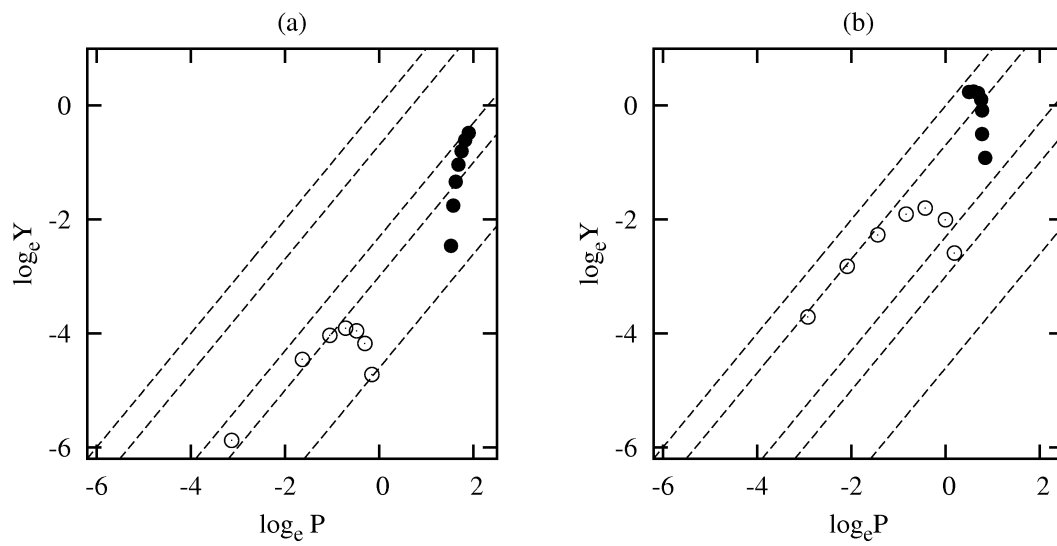


Figure 5:

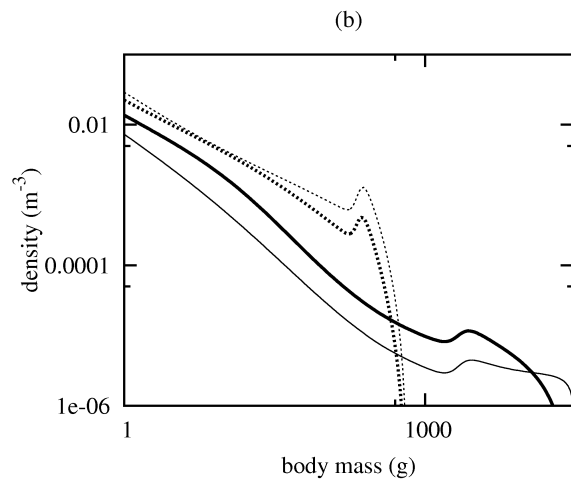
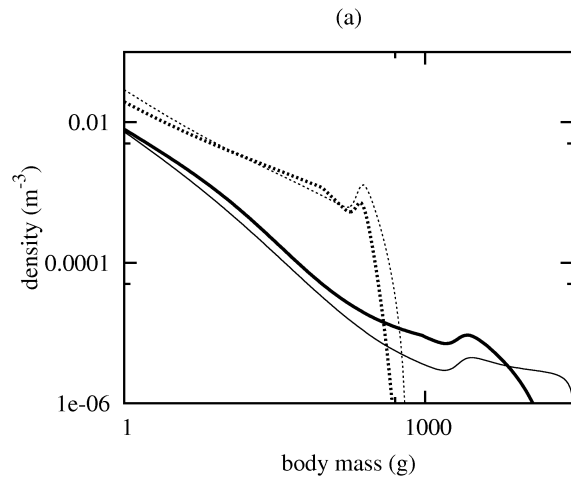


Figure 6:

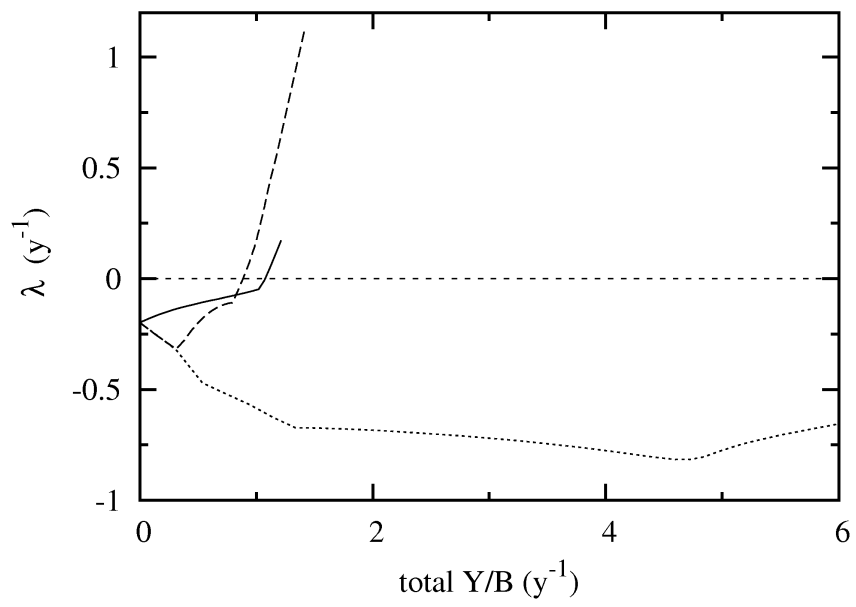


Figure 7:



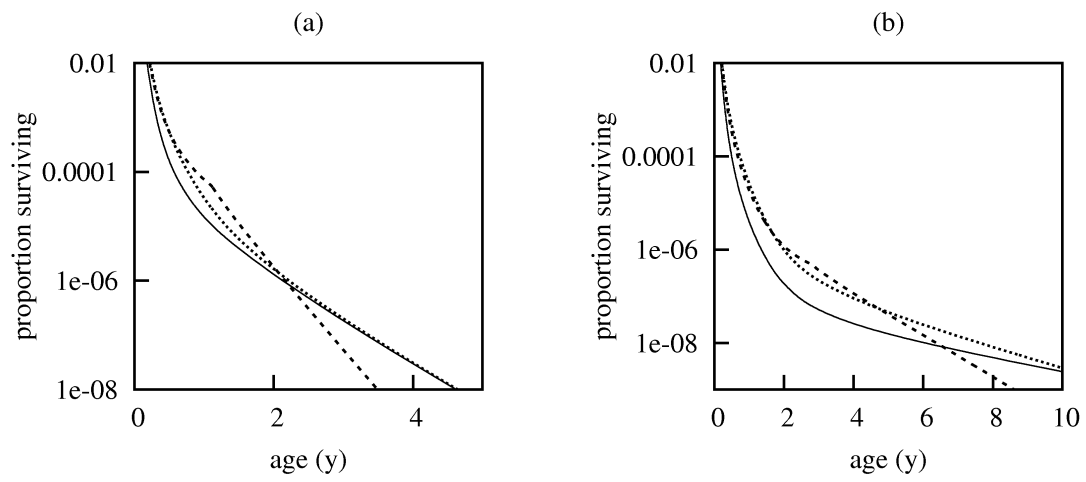


Figure 8:

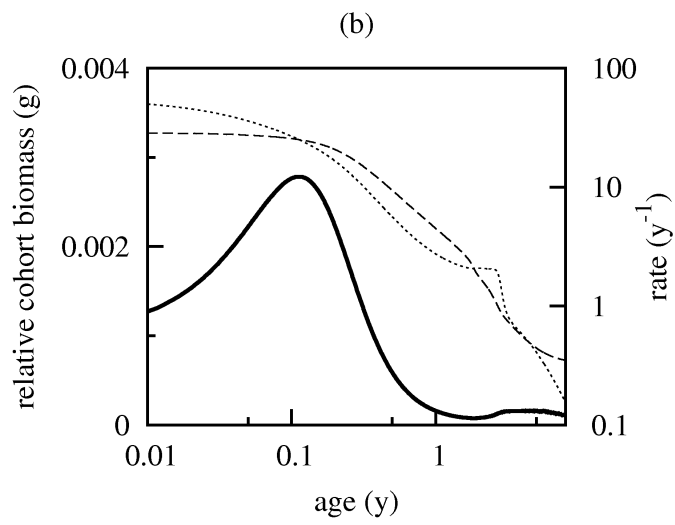
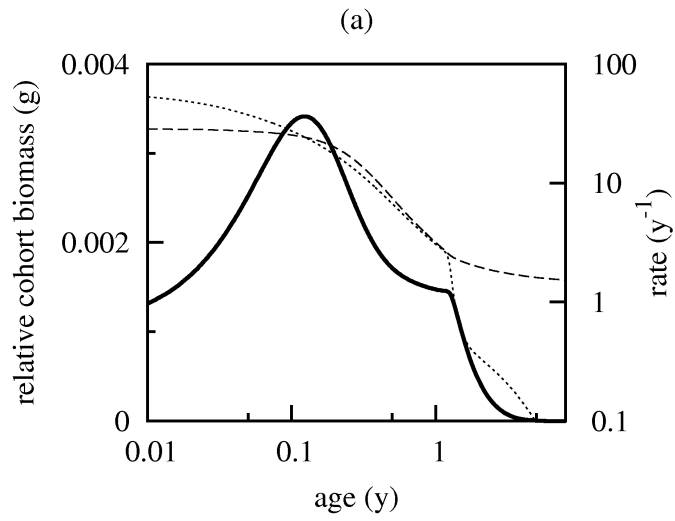


Figure 9:

# 777 Appendices

## 778 A Multispecies dynamics

779 Working from the basic jump-growth equation (Datta et al., 2010), the rate of change of  
780 density  $\phi_i(w)$  of species  $i$  at mass  $w$  is partitioned into the following components:

$$\begin{aligned}
 781 \quad \frac{\partial}{\partial t} \phi_i(w) = & \int \sum_{j=0}^n \left( \begin{array}{l} \text{growth to larger size} \\ - \overbrace{\epsilon_i(w) T_{ij}(w, w') \phi_i(w) \phi_j(w')} \\ \\ \text{death due to predation} \\ - \overbrace{T_{ji}(w', w) \phi_j(w') \phi_i(w)} \\ \\ \text{growth from smaller size} \\ + \overbrace{\epsilon_i(w - Kw') T_{ij}(w - Kw', w') \phi_i(w - Kw') \phi_j(w')} \\ \\ \text{reproduction} \\ + \overbrace{\frac{b_i(w) R_i}{2w_i}} \\ \\ \text{non-predation mortality} \\ - \overbrace{(\mu_{o,i}(w) + \mu_{f,i}(w)) \phi_i(w)} \end{array} \right) dw' \\
 782 & \\
 783 & \\
 784 & \hspace{15em} \text{(A.1)}
 \end{aligned}$$

785 where predation acts over all components in an ecosystem comprising  $n$  fish species  $j =$   
786  $1, \dots, n$ , and plankton, denoted by the index 0. All functions involving predation depend on  
787 time  $t$ , but this is suppressed for notational simplicity. For simplicity the plankton spectrum  
788 is assumed to be fixed, leaving a system of  $n$  integro-differential equations,  $i = 1, \dots, n$ , one  
789 equation for each fish species. Eq. (A.1) is not identical to previous versions of the jump-  
790 growth equation with reproduction (Law et al., 2012, 2013). We have made the change so  
791 that biomass is fully accounted for.

792 In Eq. (A.1), the function  $T_{ij}(w_1, w_2)$  describes the rate at which predators of mass  $w_1$   
793 in species  $i$  feed on prey of mass  $w_2$  in taxon  $j$ . The function  $\epsilon_i(w)$  is the proportion of  
794 predators of species  $i$  at mass  $w$  that allocate the incoming mass of prey to somatic growth  
795 as opposed to reproduction; this encodes some basic information about the species' life-  
796 history, and increases to a value 1 at the maximum body size of species  $i$ .  $K$  is the food

797 conversion efficiency. The function  $\mu_{o,i}(w)$  is species  $i$ 's per capita mortality rate at mass  $w$   
 798 due to natural causes other than predation, and  $\mu_{f,i}(w)$  is the fishing mortality rate on  $i$  at  
 799 mass  $w$ .  $R_i$  is the total mass rate at which reproductive biomass is created in species  $i$ :

$$800 \quad R_i = K \int (1 - \epsilon_i(w)) \phi_i(w) \left( \int \sum_{j=0} T_{ij}(w, w') \phi_j(w') w' dw' \right) dw, \quad (\text{A.2})$$

801 and the factor  $1/2$  in Eq. (A.1) allows for half of the mass being lost through males. The  
 802 mass of an egg is distributed as a birth kernel  $b_i(w)$ , normalized to sum to 1, here assumed  
 803 to be a Dirac- $\delta$  function corresponding to a single egg size  $w_{i,0}$  for species  $i$ .

804 Taking a Taylor expansion around  $w$  of terms in the ‘‘growth-into- $w$ ’’ expression in Eq.  
 805 (A.1), gives

$$806 \quad + (Kw')^0 \epsilon_i(w) T_{ij}(w, w') \phi_i(w) \phi_j(w')$$

$$807 \quad - (Kw')^1 \frac{\partial}{\partial w} \left[ \epsilon_i(w) T_{ij}(w, w') \phi_i(w) \phi_j(w') \right]$$

$$808 \quad + \frac{(Kw')^2}{2} \frac{\partial^2}{\partial w^2} \left[ \epsilon_i(w) T_{ij}(w, w') \phi_i(w) \phi_j(w') \right] + O(K^3). \quad (\text{A.3})$$

809 This expression is substituted into Eq. (A.1). Then a logarithmic transformation  $x =$   
 810  $\ln(w/w_0)$  of body mass is introduced, where  $w_0$  is an arbitrary body mass. This gives a new  
 811 state variable  $u_i(x) dx = \phi_i(w) dw$  with dimensions  $L^{-3}$  (Benoît and Rochet, 2004), and the  
 812 dynamics of  $u_i(x)$  are given by the partial differential equation

$$813 \quad \frac{\partial}{\partial t} u_i = - \frac{\partial}{\partial x} [\epsilon_i g_i u_i] + \frac{1}{2} \frac{\partial}{\partial x} \left[ e^{-x} \frac{\partial}{\partial x} [\epsilon_i G_i u_i] \right] + \frac{\hat{b}_i \hat{R}_i}{2} e^{-x} - (\mu_i + \mu_{o,i} + \mu_{f,i}) u_i + O(K^3), \quad (\text{A.4})$$

814 where the argument  $x$  has been omitted from each function, and  $\hat{b}_i(x) dx = b_i(w) dw$ ,  $\hat{R}_i =$   
 815  $R_i/w_0$ . We include terms up to second order here, going a step beyond the approximation of  
 816 the size-based McKendrick–von Foerster equation (Datta et al., 2010, 2011). The numerical  
 817 results in this paper are based on this equation.

818 Some extra information about the feeding rate  $T_{ij}$  is introduced (Benoît and Rochet, 2004;

819 Andersen and Beyer, 2006; Datta et al., 2010) so that, after transformation,

$$820 \quad T_{ij}(x, x') = A_i e^{\alpha_i x} s_i(e^{x-x'}) \theta_{ij}. \quad (\text{A.5})$$

821 Here the volume searched per unit time by a predator of species  $i$  at size  $x$  is written as  
 822  $A_i e^{\alpha_i x}$ , to make it scale with body size (Ware, 1978). The term  $s_i(e^{x-x'})$  is a dimensionless  
 823 feeding kernel for predator species  $i$ , dependent on the predator-prey mass ratio  $w/w' = e^{x-x'}$   
 824 (Ursin, 1973), and we assume that  $s_i(e^{x-x'}) = 0$  if  $x' > x$ , on the grounds that predators are  
 825 typically larger than their prey. The dimensionless parameter  $\theta_{ij}$  is the preference of  $i$  for  
 826 prey of type  $j$  relative to prey of type  $i$  (Hartvig et al., 2011). Thus  $\theta_{ij} = 1$ , if predation is  
 827 indiscriminate across prey species. Alternatively, it could have a smaller value to allow for,  
 828 say, spatial separation of  $j$  from  $i$  that makes encounters with  $j$  relatively rare. If  $i$  does not  
 829 encounter  $j$ ,  $\theta_{ij} = 0$ .

830 Using Eq. (A.5) in Eq. (A.4), the function  $\mu_i(x)$  is the per capita death rate of species  $i$   
 831 at size  $x$ , due to predation by all fish species

$$832 \quad \mu_i(x) = \sum_{j=1}^n A_j \theta_{ji} \int e^{\alpha_j x'} s_j(e^{x'-x}) u_j(x') dx'. \quad (\text{A.6})$$

833 The function  $g_i(x)$  is the mass specific growth rate of species  $i$  at size  $x$  from eating prey of  
 834 all taxa, before partitioning it between somatic growth and reproduction

$$835 \quad g_i(x) = A_i K e^{(\alpha_i - 1)x} \sum_{j=0}^n \theta_{ij} \int e^{x'} s_i(e^{x-x'}) u_j(x') dx'. \quad (\text{A.7})$$

836  $G_i(x)$  is the corresponding rate function for the second-order diffusion term

$$837 \quad G_i(x) = A_i K^2 e^{(\alpha_i - 1)x} \sum_{j=0}^n \theta_{ij} \int e^{2x'} s_i(e^{x-x'}) u_j(x') dx'. \quad (\text{A.8})$$

838 The intrinsic mortality rate  $\mu_{o,i}(x)$  accounts for sources of mortality other than predation  
 839 and fishing. We assume that this is proportional to the mass-specific needs for metabolism,  
 840 relative to the mass-specific rate at which food becomes available at size  $x$ . These rates are

841 set relative to their values at egg size, so  $\mu_{o,i}(x_{i,0}) = \mu_{o,i}^{(0)}$  is a fixed baseline intrinsic mortality  
 842 at birth for species  $i$ . The metabolic need should scale with body mass, and we write this  
 843 as  $\exp(-\xi(x - x_{i,0}))$ , using the same exponent for all species. The mass specific rate of food  
 844 intake at size  $x$  relative to size  $x_{i,0}$  is  $g_i(x)/g_i(x_{i,0})$ . Thus

$$845 \quad \mu_{o,i}(x) = \mu_{o,i}^{(0)} \exp(-\xi(x - x_{i,0})) g_i(x_{i,0})/g_i(x), \quad (\text{A.9})$$

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

847 The function  $\epsilon_i(x)$  is defined in terms of allocation of incoming mass to reproduction,  
 848 using a form suggested by Hartvig et al. (2011):

$$849 \quad 1 - \epsilon_i(x) = \left[ 1 + \exp(-\rho_{i,m}(x - x_{i,m})) \right]^{-1} \exp(\rho(x - x_{i,\infty})). \quad (\text{A.10})$$

850 Here  $w_0 e^{x_{i,m}}$  is the body mass at which 50 % of the fish of species  $i$  are mature, and  $\rho_{i,m}$   
 851 defines the body-mass range over which fish are maturing. The asymptotic body mass  $w_0 e^{x_{i,\infty}}$   
 852 is the size at which all incoming mass is allocated to reproduction and no further somatic  
 853 growth is possible, the approach to this size being scaled by a parameter  $\rho$  common to all  
 854 species.

855 The egg size  $x_{i,0}$  and asymptotic size  $x_{i,\infty}$  together give boundary conditions for Eq. (A.4),  
 856 over which there is no flux of individuals. In other words, individuals cannot grow from size  
 857  $x_i < x_{i,0}$  to  $x_i > x_{i,0}$  nor shrink from size  $x_i > x_{i,0}$  to  $x_i < x_{i,0}$ , with a similar condition at  
 858 the upper boundary. Mathematically, these boundary conditions are written as follows

$$859 \quad J(x_{i,0}) = J(x_{i,\infty}) = 0, \quad (\text{A.11})$$

860 where the flux  $J$  is the sum of the advective and diffusive fluxes in Eq. (A.4):

$$861 \quad J(x) = \epsilon_i(x) g_i(x) u_i(x) - \frac{1}{2} e^{-x} \frac{\partial}{\partial x} (\epsilon_i(x) G_i(x) u_i(x)). \quad (\text{A.12})$$

862 For simplicity, we do not deal with the dynamics of the plankton. This can be thought

863 of as an assumption that the plankton operate on a short time scale relative to the fish  
864 community. For instance, if a semi-chemostat model is used

$$865 \quad \frac{\partial}{\partial t} u_0(x, t) = \frac{1}{\tau} (f(x) - u_0(x, t)) - \text{predation}, \quad (\text{A.13})$$

866 there is a limit at  $\tau = 0$  in which  $u_0(x, t) = f(x)$  for all  $t$ , equivalent to our model. The fixed  
867 plankton spectrum was taken as  $u_0(x) = f(x) = u_{0,0} \exp^{(1-\gamma)x}$ , where  $u_{0,0}$  is the plankton  
868 abundance at 1 mg, giving a power-law relationship between body mass and abundance.

## 869 **B Numerics**

870 Parameter values were set to match approximately the life histories of mackerel and cod.

871 Mackerel egg mass was obtained from a diameter 1.24 mm (Mendiola et al., 2006) and  
872 specific gravity 1.02 (Coombs, 1981), giving a mass 0.8 mg, which we rounded to 1 mg.  
873 Maturation occurs around age 2 y, when body mass is approximately 200 g (ICES, 2013a);  
874 we therefore took the body size at which 50 % of individuals are mature as 200 g. With  
875 a value  $\rho_{1,m} = 15$ , maturation was starting at approximately 170 g. Villamor et al. (2004)  
876 give average parameters for the von Bertalanffy growth equation of mackerel as  $L_\infty = 42.7$   
877 cm,  $k = 0.268 \text{ y}^{-1}$ , and  $t_0 = -2.17 \text{ y}$ . To convert from length  $l$  (cm) to mass  $w$  (g), we  
878 used an allometric relation  $w = 0.0064l^{3.079}$  (Santos et al., 2002), giving an approximate  
879 asymptotic mass of 650 g. The von Bertalanffy growth equation is unable to fit mackerel's  
880 fast growth in its first year, and has to make  $t_0$  strongly negative. This issue does not arise  
881 in the growth trajectory of the size-spectrum model, if the volumetric search-rate parameter  
882  $A_i$  is made sufficiently large (Hunter, 1981); we set this at  $750 \text{ m}^3 \text{ y}^{-1} \text{ g}^{-\alpha}$ , in contrast to  
883 a value 600 in Law et al. (2012, 2013). The feeding kernel of mackerel was centred on a  
884 predator:prey body size ratio 400:1 ( $\beta = 6$ ); this weights mackerel towards a planktivorous  
885 habit relative to cod (Olaso et al., 2005), the majority of its diet being in the size range  
886 of plankton until a body mass of approximately 10 g is reached. For simplicity, the diet  
887 breadth parameter  $\sigma$  was set at 2.5; a significantly smaller value would have destabilized the

888 single-species mackerel subsystem, creating a more complicated periodic solution. There was  
889 no discrimination between prey taxa at a given prey size, i.e.  $\theta_{1,0} = \theta_{1,1} = \theta_{1,2} = 1$ .

890 Cod egg mass was obtained from an average diameter of 1.6 mm (Chambers and Waiwood,  
891 1996) and an assumption of neutral buoyancy, to give an average egg mass of 1.6 mg, which  
892 we rounded to 1 mg. We took a value for 50 % maturity at 2 kg, and an asymptotic mass at  
893 30 kg (Bogstad, personal communication). With a value  $\rho_{2,m} = 8$ , maturation was starting  
894 at approximately 1.5 kg. Limburg et al. (2008) (Supplement) give average von Bertalanffy  
895 parameters for Baltic cod in 1995 as  $L_\infty = 137.6$  cm,  $k = 0.1223$   $y^{-1}$ , and  $t_0 = 0.3115$  y,  
896 and we use an allometric relation  $w = 0.009l^{3.00}$  for conversion to mass (Bogstad, personal  
897 communication). We set the food searching parameter  $A_i$  for cod somewhat smaller than that  
898 for mackerel, at  $700$   $m^3$   $y^{-1}$   $g^{-\alpha}$ , to match its slower growth when small. The feeding kernel  
899 of cod was centred on a predator:prey body size ratio 90:1 ( $\beta = 4.5$ ), with a diet breadth  
900  $\sigma = 1.9$ , based on information from Georges Bank cod given in Table 4.1 of Blanchard (2008).  
901 There was no discrimination between prey taxa at a given prey size, i.e.  $\theta_{2,0} = \theta_{2,1} = \theta_{2,2} = 1$ .

902 In setting parameter values for the intrinsic mortality rate  $\mu_{o,i}(x)$ , we note that metabolic  
903 rate is unlikely to scale with body size with an exponent -0.25 in fish (equivalent to +0.75 per  
904 individual of Kleiber's law). Killen et al. (2007) reported exponents for standard metabolic  
905 rate in three species of fish around -0.17, rising to around -0.1 as metabolic activity increased  
906 in keeping with a broader meta-analysis of ectotherms (Glazier, 2009) (we have made the  
907 transformation to mass-specific scalings here by subtracting 1). We therefore assumed a value  
908  $\xi = -0.15$ . A low value  $\mu_{o,i}^{(0)} = 0.1$   $y^{-1}$  was used for for the intrinsic mortality rate at birth  
909 for both species, so that most mortality would come from predation.

910 The lower limit of body size for the plankton was set at  $\exp(-20)$  of the fish egg mass.  
911 i.e.  $4.8 \times 10^{-11}$  g, to ensure a good coverage for the mackerel feeding kernel for the smallest  
912 larvae, and we allowed some overlap of the plankton spectrum with the fish spectra by setting  
913 the upper size limit at 0.03 g. We set the density of plankton at 1 mg,  $u_{0,0}$ , to a value 100  
914  $m^{-3}$ , based on interpolation from San Martin et al. (2006, Figure 2c), and took the standard  
915 assumption that abundance scales with body mass with an exponent  $\gamma = 2$  (San Martin  
916 et al., 2006).



917 Numerical computation of the steady state was done in two steps. First, a numerical  
 918 integration of Eq. (A.4) was carried out to get near to the steady state (in some cases the  
 919 steady state was not an attractor). Then a Newton-Raphson algorithm was used to solve  
 920 for the steady state and to obtain information on its local asymptotic stability through the  
 921 eigenvalues of the Jacobian matrix. The stability of dynamic size spectra is sensitive to the  
 922 discretization of body mass, so we used as small a step size as possible. This was  $dx = 0.05$   
 923 unless otherwise stated.

## 924 C Mass balance at steady state

925 Consider the steady state at which the right-hand side of Eq. (A.4) is zero, writing the  
 926 steady-state density for species  $i$  as  $\hat{u}_i(x)$ . We include terms in Eq. (A.4) up to first order.  
 927 It is possible to include second-order terms and this results in a slightly modified expression  
 928 for the total productivity  $P_i$  of species  $i$ ; numerically this makes a negligible difference to  
 929 the value of  $P_i$ . Multiplying Eq. (A.4) through by the body mass  $w_0 e^x$  and integrating from  
 930  $x = x_{i,0}$  to  $x = x_{i,\max}$  gives:

$$931 \quad 0 = - \int w_0 e^x (\mu_i + \mu_{o,i} + \mu_{f,i}) u_i dx - \int w_0 e^x \frac{d}{dx} (\epsilon_i g_i u_i) dx + \int w_0 \frac{\hat{R}_i \hat{b}_i}{2} dx \quad (\text{C.1})$$

932 We retain  $w_0$  in these expressions so that the mass flows all have the standard dimensions  
 933 ( $\text{M L}^{-3} \text{T}^{-1}$ ). The first integral in this equation is the total rate at which biomass is being  
 934 lost from species  $i$  due to mortality. This can be decomposed into the rate of biomass loss  
 935 to predation mortality, which we write as  $D_i$ , the rate of biomass loss to intrinsic mortality,  
 936 which we write as  $D_{o,i}$  and rate of biomass loss to fishing mortality, which is equivalent to the  
 937 yield,  $Y_i$ . Using integration by parts on the second integral and the fact that  $\hat{b}_i$  is a Dirac- $\delta$   
 938 function, we have

$$939 \quad 0 = -D_i - D_{o,i} - Y_i - [w_0 e^x \epsilon_i g_i u_i]_{x_{i,0}}^{x_{i,\infty}} + \int w_0 e^x \epsilon_i g_i u_i dx + w_0 \frac{\hat{R}_i}{2}. \quad (\text{C.2})$$

940 The boundary conditions (A.11) mean that there is no contribution from the term  $[e^x \epsilon_i g_i u_i]_{x_i,0}^{x_i,\infty}$ .  
 941 The remaining integral is the total rate at which biomass is being accumulated due to somatic  
 942 growth of species  $i$ , i.e. the total productivity  $P_i$ . Thus the overall balance for species  $i$  at  
 943 steady state is:

$$944 \quad P_i + R_i/2 = D_i + D_{o,i} + Y_i. \quad (\text{C.3})$$

945 The term  $R_i/2$  is a net flow of mass to reproduction, after loss of the male component. So  
 946 the full balance between gains and losses is:

$$947 \quad P_i + R_i = D_i + D_{o,i} + Y_i + R_i/2. \quad (\text{C.4})$$

948 Each term in this equation is a rate of mass flow ( $\text{M L}^{-3} \text{T}^{-1}$ ) measured at the population  
 949 level for species  $i$ . The terms on the left-hand side correspond to processes that generate new  
 950 biomass (somatic growth and reproduction) and those on the right-hand side correspond  
 951 to processes that cause loss of biomass, i.e. mortality and the contribution of males to  
 952 reproduction. Terms in this equation involving predation can be disaggregated down to the  
 953 mass flow corresponding to each prey or predator species; the totals used above are the sum  
 954 of these components:  $P_i = \sum_j P_{ij}$ ,  $R_i = \sum_j R_{ij}$ , and  $D_i = \sum_j D_{ji}$ .

955 For reference purposes, the general version of this that includes the diffusive terms looks  
 956 like this:

$$957 \quad 0 = - \int e^x (\mu_i + \mu_{o,i} + \mu_{f,i}) u_i dx - \int e^x \frac{dJ}{dx} dx + \int \frac{\hat{R}_i \hat{b}_i}{2} dx$$

$$958 \quad = -D_i - D_{o,i} - Y_i - w_0 [e^x J]_{x_i,0}^{x_i,\infty} + w_0 \int e^x J dx + \frac{R_i}{2}, \quad (\text{C.5})$$

959 where  $J$  is given by Eq. (A.12). The boundary conditions (A.11) specify that  $J(x_{i,0}) =$   
 960  $J(x_{i,\infty}) = 0$ , so there is no contribution from the boundary term. The productivity is  
 961 given by the remaining integral,  $\int e^x J dx$ , as this is the net rate of biomass accumulation for  
 962 species  $i$ , summed over all body sizes. We therefore have the same mass balance equation as

963 previously, Eq. (C.4), but with a different expression for the productivity:

$$\begin{aligned}
964 \quad P_i &= w_0 \int e^x J dx \\
965 &= w_0 \int e^x \left( \epsilon_i g_i u_i - \frac{1}{2} e^{-x} \frac{d}{dx} (\epsilon_i G_i u_i) \right) dx \\
966 &= w_0 \int e^x \epsilon_i g_i u_i dx - \frac{w_0}{2} [\epsilon_i G_i u_i]_{x_{i,0}}^{x_{i,\infty}} \\
967 &= w_0 \int e^x \epsilon_i g_i u_i dx + \frac{w_0}{2} G_i(x_{i,0}) u_i(x_{i,0}), \tag{C.6}
\end{aligned}$$

968 where the last line results from the fact that  $\epsilon_i(x_{i,\infty}) = 0$  and  $\epsilon_i(x_{i,0}) = 1$ . Numerically, the  
969 “correction term”  $G_i(x_{i,0}) u_i(x_{i,0}) w_0 / 2$  is very small ( $< 0.1\%$ ) compared to the main integral  
970 term.

## 971 D Multispecies harvesting

972 Yields  $Y_i$ , from harvesting species  $i$  in a multispecies ecosystem are based on the equation:

$$973 \quad Y_i = \int w_0 e^x \mu_{f,i}(x) u_i(x) dx, \tag{D.1}$$

974 where fishing mortality  $\mu_{f,i}(x)$  is set to an appropriate pattern of fishing over body size  $x$ , as  
975 required. We use the following patterns of fishing mortality.

- 976 • **Figure 3.** For a size-at-entry fishery, a simple assumption is that  $\mu_{f,i}(x) = F_i$ , once  
977 fish of species  $i$  have grown to the minimum size of fishing  $\underline{x}_i$ . Then the yield is:

$$978 \quad Y_i = F_i \int_{\underline{x}_i}^{\bar{x}_i} w_0 e^x u_i(x) dx = F_i B_i^*, \tag{D.2}$$

979 where  $B_i^*$  is the stock biomass integrated from the size-at-entry to the maximum size  
980  $\bar{x}_i$ .

981 • **Figure 4a.** A size-at-entry fishery can be balanced by choosing the  $F_i$ s so that both  
 982 species have the same value of  $Y_i/P_i$ . Using Eq. (D.2), this is achieved by setting  
 983 fishing mortality from the size-at-entry onwards as

$$984 \quad \mu_{f,i}(x) = F_i = c_1 \frac{P_i}{B_i^*}, \quad (\text{D.3})$$

985 where  $c_1$  is the constant of proportionality, and  $P_i$  is the productivity from somatic  
 986 growth, as given in Eq. (C.4).

987 • **Figure 4b.** An alternative way of balancing a size-at-entry fishery is to weight the  
 988 fishing mortality by its productivity under the current exploitation:

$$989 \quad \mu_{f,i}(x) = F_i = c_2 P_i, \quad (\text{D.4})$$

990 where  $c_2$  is a constant of proportionality that can be altered to change the overall  
 991 intensity of fishing.

992 • **Figure 5a.** A simple way to balance size-specific harvesting to a component of pro-  
 993 ductivity is to make fishing proportional to the mass-specific, somatic, growth rate:

$$994 \quad \mu_{f,i}(x) = c_3 \epsilon_i(x) g_i(x), \quad (\text{D.5})$$

995 where  $c_3$  is a constant of proportionality that remains the same across all harvested  
 996 sizes of all species, but that can be altered to change the overall intensity of fishing.  
 997 This has the effect of ensuring that all species have the same value of  $Y_i/P_i^*$ , because

$$998 \quad \frac{Y_i}{P_i^*} = \frac{\int_{\underline{x}_i}^{\bar{x}_i} w_0 e^x c_3 \epsilon_i(x) g_i(x) u_i(x) dx}{\int_{\underline{x}_i}^{\bar{x}_i} w_0 e^x \epsilon_i(x) g_i(x) u_i(x) dx} = c_3. \quad (\text{D.6})$$

999 Notice that the productivity  $P_i^*$  must be measured over the size range of exploitation  
 1000 for this result to be exact.

1001 • **Figure 5b.** The full balancing to productivity at every body size of every species is:

$$1002 \quad \mu_{f,i}(x) = c_4 w_0 e^x \epsilon_i(x) g_i(x) u_i(x), \quad (\text{D.7})$$

1003 where  $c_4$  is a constant of proportionality that can be altered to change the overall  
1004 intensity of fishing.

1005 Note that most of these harvest patterns use information on the current status of the  
1006 exploited species, such as its productivity and biomass. We take this information from the  
1007 species populations at each step of numerical integration, and as the numerical analysis  
1008 searches for the steady state. The measures that provide this information are themselves  
1009 functions of time, and settle to fixed values when the steady state  $\hat{u}_i(x)$  is reached. All  
1010 results are reported at the steady state.

## 1011 E Body size maximizing productivity and cohort biomass

1012 Consider the steady state at which the right-hand side of Eq. (A.4) is zero, writing the steady-  
1013 state density for species  $i$  as  $\hat{u}_i(x)$ . We take the first-order terms from Eq. (A.4), leaving out  
1014 the diffusion term and higher-order terms:

$$1015 \quad 0 = -\mu_{\text{tot},i}(x) \hat{u}_i(x) - \frac{\partial}{\partial x} [\epsilon_i(x) g_i(x) \hat{u}_i(x)]. \quad (\text{E.1})$$

1016 All mortality terms have been lumped together, so  $\mu_{\text{tot},i} = \mu_i + \mu_{o,i} + \mu_{f,i}$ , and the reproduction  
1017 term has been omitted, as this only operates at the smallest body size  $x_0$ . Dividing through  
1018 by  $\epsilon_i(x) g_i(x) \hat{u}_i(x)$  puts the second term into a standard form for integration, giving

$$1019 \quad 0 = - \int_{x_{i,0}}^x \frac{\mu_{\text{tot},i}(y)}{\epsilon_i(y) g_i(y)} dy - \left[ \ln [\epsilon_i(x) g_i(x) \hat{u}_i(x)] \right]_{x_{i,0}}^x. \quad (\text{E.2})$$

1020 Removing the logarithm, and multiplying through by body mass  $w_0 e^x$ , gives

$$1021 \quad w_0 e^{x_0} \frac{p_i(x)}{p_i(x_{i,0}^+)} = w_0 e^x \exp \left( - \int_{x_{i,0}}^x \frac{\mu_{\text{tot},i}(y)}{\epsilon_i(y) g_i(y)} dy \right), \quad (\text{E.3})$$

1022 where  $p_i(x) = w_0 e^x \epsilon_i(x) g_i(x) \hat{u}_i(x)$  is productivity at size  $x$  and  $p_i(x_{i,0}^+) = \lim_{x \downarrow x_0} p_i(x)$ .

1023 Note that the rate of change of body size with respect to age  $a$  is  $dx/da = \epsilon_i(x) g_i(x)$ .  
1024 So the exponential term in Eq. E.3 is the proportion of individuals in a cohort surviving  
1025 from birth at size  $x_{i,0}$  up to age  $a$  (and size  $x$ ). Multiplying the integral by  $w_0 e^x$ , gives the  
1026 cohort biomass at age  $a$  (and size  $x$ ) per newborn individual,  $B_{c,i}(a)$ . By this argument, we  
1027 establish a proportionality between the productivity at body size  $x$ , and the cohort biomass  
1028 at age  $a$  (corresponding to size  $x$ ), i.e.  $p_i(x) \propto B_{c,i}(a)$ .

1029 To find turning points, we differentiate  $p_i(x)$  with respect to size  $x$  and set the derivative  
1030 to zero:

$$1031 \quad 0 = e^x \frac{d}{dx} [\epsilon_i(x) g_i(x) \hat{u}_i(x)] + e^x \epsilon_i(x) g_i(x) \hat{u}_i(x) \quad (\text{E.4})$$

1032 From Eq. (E.1), the derivative in Eq. (E.4) must equal  $-\hat{u}_i(x) \mu_{\text{tot},i}(x)$ . Thus, in the  
1033 steady-state ecosystem, turning points for  $p_i(x)$  (and hence  $B_{c,i}(a)$ ) occur at points where  
1034  $\mu_{\text{tot},i}(x) = \epsilon_i(x) g_i(x)$ . In other words, there is a turning point for both  $p_i(x)$  and  $B_{c,i}(a(x))$   
1035 when a body size  $x^*$  is reached at which the sum of all mortality rates equals the mass-specific  
1036 somatic growth rate. The turning point is a maximum if  $d/dx(\mu_{\text{tot},i}) > d/dx(\epsilon_i g_i)$ . Note that  
1037 a turning point does not necessarily exist in a feasible range of body sizes; for instance, a  
1038 power-law steady state has the same exponent for predation mortality and growth rate, in  
1039 which case  $d/dx(\mu_{\text{tot},i}) = dg_i/dx$  for all  $x$ . Note also that, because growth and mortality are  
1040 nonlinear functions, there may be more than one turning point.