

Interacting forces of predation and fishing affect species' maturation size

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Summary

1. Fishing is a strong selective force and is supposed to select for earlier maturation at smaller body size. However, the extent to which fishing-induced evolution is shaping ecosystems remains debated. This is in part because

it is challenging to disentangle fishing from other selective forces (e.g. size-structured predation and cannibalism) in complex ecosystems undergoing rapid change.

2. Changes in maturation size from fishing and predation have previously been explored with multi-species physiologically structured models but assumed separation of ecological and evolutionary timescales. To assess the eco-evolutionary impact of fishing and predation at the same timescale, we developed a stochastic physiologically size-structured food web model, where new phenotypes are introduced randomly through time enabling dynamic simulation of species' relative maturation sizes under different types of selection pressures.
3. Using the model, we carried out a fully factorial *in silico* experiment to assess how maturation size would change in the absence and presence of both fishing and predation (including cannibalism). We carried out ten replicate stochastic simulations exposed to all combinations of fishing and predation in a model community of nine interacting fish species ranging in their maximum sizes from 10g to 100kg. We visualised and statistically analysed the results using linear models.
4. The effects of fishing on maturation size depended on whether or not predation was enabled and differed substantially across species. Fishing consistently reduced the maturation sizes of two largest species whether or not predation was enabled and this decrease was seen even at low fishing intensities ($F = 0.2yr^{-1}$). In contrast, the maturation sizes of the three smallest species evolved to become smaller through time but this happened regardless

of the levels of predation or fishing. For the four medium-size species, the effect of fishing was highly variable with more species showing significant and larger fishing effects in the presence of predation.

5. Ultimately our results suggest that the interactive effects of predation and fishing can have marked effects on species' maturation sizes, but that, at least for the largest species, predation does not counterbalance the evolutionary effect of fishing. Our model also produced relative maturation sizes that are broadly consistent with empirical estimates for many fish species.

Keywords

body size, coexistence, evolution, fisheries, food webs, multi-species size spectrum model

Introduction

1 The last century has been marked by a rapid decline in the health of many
2 ecosystems due to exploitation, invasive species, climate change, pollution and eu-
3 trophication ([Smith, 2003](#); [Halpern et al., 2008](#)). These drivers represent strong
4 selective pressures, and rapid evolutionary responses have been documented in
5 many organisms and ecosystems ([Palumbi, 2001](#); [Darimont et al., 2009](#); [Sullivan](#)
6 [et al., 2017](#)). In marine ecosystems one of the major ecological and evolution-
7 ary forces is fishing ([Jorgensen et al., 2007](#); [Audzijonyte et al., 2016](#); [Fugère and](#)
8 [Hendry, 2018](#)). Fishing can alter body size structure, size specific mortality, opti-
9 mal life histories, and lead to evolution towards earlier maturation, smaller adult

body sizes, and altered behaviour (Conover and Munch, 2002; Audzijonyte et al., 2013a; Therkildsen et al., 2013). Evolution of maturation and body size in response to size selective fishing has been demonstrated in experimental studies (Conover and Munch, 2002; Uusi-Heikkilä et al., 2015) and single species models (de Roos et al., 2006; Enberg et al., 2009). However, outcomes of experimental studies cannot be easily extrapolated to real ecosystems, because it is unclear how ecological and evolutionary feedbacks through species interactions might modify selection pressures imposed by fishing (Kuparinen and Merilä, 2007).

Life-history theory makes it clear that increased adult mortality will select for earlier maturation (Charnov et al., 2013). Although wild fish stocks around the world have been observed to follow a trend towards earlier maturation and smaller maximum body size (Olsen et al., 2005; Audzijonyte et al., 2013b, 2016), debate remains as to whether this can be explained by fishing induced evolution (FIE) (van Rijn et al., 2017). Multiple drivers can affect maturation and body size and similar changes are also observed and expected in response to increased water temperatures (Blanchard et al., 2005; Baudron et al., 2014; Audzijonyte et al., 2016). The combined effect of these pressures on trait evolution is not straightforward to predict. For example, high predation can also drive evolution to earlier maturation in wild populations (Reznick et al., 1997, 2008) and predation on small individuals may override evolutionary selection from low fishing intensity, and even drive an increase in maturation size (Edeline et al., 2007). Furthermore, increased and decreased maturation size were both observed in a single predator-single prey model, that included competition and cannibalism, when increased mortality was applied to small individuals; this is because change in maturation size proved to be dependent on how mortality changed with body size (Claessen et al., 2002;

35 [Gårdmark et al., 2003](#)). As fishing pressure increased in many intensively har-
36 vested areas, predation mortality has declined substantially, due to large changes
37 in the biomasses and size structure of top predators ([Fisher et al., 2010](#)), leading to
38 large effects on the abundance of smaller species (e.g. [Shackell et al. 2010](#)). These
39 studies suggest that a universal decrease in maturation size in response to fishing
40 may be unlikely in complex multi-species ecosystems, where multiple species are
41 fished and interact through predation and competition. Understanding and pre-
42 dicting FIE in a multispecies context therefore requires better representation of
43 the potential interactions between fishing and other ecological selection forces.

44 The debate on the universality of FIE has important implications for pre-
45 cautionary fisheries management. If evolutionary responses to fishing are unpre-
46 dictable and varied, it is unrealistic to expect its inclusion in forecasts of stock
47 productivity. It would also mean that the widespread trends towards earlier mat-
48 uration in many harvested stocks could be caused by factors other than, or in
49 addition to, fishing (e.g. climate change) (see [Audzijonyte et al. 2016](#); [van Rijn](#)
50 [et al. 2017](#)). On the other hand, if under most conditions fishing does select for
51 earlier maturation at smaller body size in multi-species systems, fisheries managers
52 should be encouraged to account for such trends in their management plans. To
53 address the role of species interactions and eco-evolutionary feedbacks on the evo-
54 lution of fish maturation size under fishing we used a multi-species size spectrum
55 model with temporal adaptive evolution of maturation size. The need for this
56 kind of model is well recognised (e.g. [Fraser 2013](#)), yet most marine ecosystem
57 and multi-species models do not include selection-driven (as opposed to random)
58 evolutionary changes ([Belgrano and Fowler, 2013](#)).

59 Individual body size is widely accepted as one of the most important functional

60 traits, especially in marine ecosystems, and size spectrum food web models have
61 been successfully applied to study changes in individual body size distributions
62 of communities and ecosystems ([Blanchard et al., 2017](#)). Size spectrum models
63 can resolve the detailed demography of species by characterizing maturation and
64 asymptotic sizes, as well as enabling given sizes of particular species to interact with
65 other sizes and species through predation (including cannibalism) and competition
66 ([Hartvig and Andersen, 2013](#)).

67 The inclusion of maturation size in size spectrum models makes them partic-
68 ularly useful for addressing questions related to adaptive maturation responses to
69 fishing. Indeed these kinds of models have previously been coupled with adap-
70 tive dynamics models to explore the long-term effects of different selective forces
71 on maturation sizes. For example, interference competition, in combination with
72 predation but without fishing, has been shown to influence the distribution and di-
73 versity of maturation sizes at equilibrium in a modelled community size spectrum
74 ([Zhang et al., 2015](#)). Fisheries-induced evolution has also been studied using a sim-
75 ilar modelling framework. [Law and Plank \(2018\)](#) used a two species size spectrum
76 model to explore the effects of different size-structured harvesting strategies on
77 maturation size changes, emphasising the importance of including both intra- and
78 inter-specific predation. They also suggested that to usefully inform contemporary
79 fisheries management, closer examination of the intricacies of multi-species systems
80 at shorter time-scales would be warranted ([Law and Plank, 2018](#)). The adaptive
81 dynamics approach used in these and other models ([Dieckmann and Law, 1996](#);
82 [Gårdmark et al., 2003](#)) assumes a separation of ecological and evolutionary time
83 scales, with fast ecological dynamics influencing selection acting on species and size
84 classes and the introduction of new species occurring at equilibrium. However, ev-

85 idence of rapid evolution and eco-evolutionary feedbacks is well recognised and
86 ubiquitous ([Ellner, 2013](#); [Matthews et al., 2016](#); [Beckerman et al., 2016](#)), meaning
87 that ecology and evolution happens on the same time scales.

88 Inspired by the above adaptive dynamics studies, we develop a model that al-
89 lows us to investigate the consequences of traits adapting and changing through
90 time, but with the introduction of new phenotypes occurring at the same timescale
91 as the ecological processes of feeding, growth, mortality and reproduction. We have
92 extended the physiologically structured multi-species size spectrum modelling ap-
93 proach to explore temporal eco-evolutionary dynamics of maturation size and its
94 response to fishing. With this model we tackle the central questions regarding
95 FIE, namely whether and how ecological interactions (e.g. intra- and inter-specific
96 predation) affect fisheries-induced selection pressures on maturation size ([Kupari-
97 nen and Merilä, 2007](#); [Edeline et al., 2007](#); [Carlson et al., 2007](#)). We ask three
98 main questions. Does, in accordance with single species predictions, FIE lead to
99 universally declining maturation size? How does the interaction of fishing ver-
100 sus predation (and cannibalism) pressure affect the emergent maturation size for
101 species of different asymptotic sizes and hence different trophic roles? What is the
102 minimum fishing intensity necessary to trigger FIE responses in maturation size?

103 We expect that strong size-selective fishing will select for earlier maturation
104 size. However, we expect that predation (which for our purposes includes can-
105 nibalism) will also lead to changes in maturation size, but that the direction of
106 these changes is harder to predict because predatory interactions are more com-
107 plex than the pressures arising from size-selective fisheries. We explore whether
108 predation can counterbalance the evolutionary pressure from fishing in species at
109 different trophic levels and assess at what level of intensity fishing becomes the

110 overpowering selective force.

111 Methods

112 In this study we explore the eco-evolutionary feedbacks between fishing, com-
113 munity dynamics and dynamic temporal changes (evolution) in maturation size.
114 To model community dynamics we used a modified version of the trait-based size
115 spectrum model (Andersen and Pedersen, 2010; Hartvig et al., 2011) implemented
116 in the R package “mizer” (Scott et al. 2014; which also provides further documen-
117 tation). Our modifications to “mizer” include the introduction of eco-evolutionary
118 dynamics (the code is available on <https://github.com/baldrech/MizerEvo>). The
119 modelling approach has two components: 1) an ecological component, which de-
120 fines intra- and inter-specific interactions that act as selective forces influencing sur-
121 vival and community dynamics (i.e. as in the basic “mizer” package), and 2) an evo-
122 lutionary component that generates random new trait values (i.e. maturation size),
123 which are introduced in the community at each time step. A conceptual model il-
124 lustration is shown in Fig.1 and below we describe the key components of the model
125 with equations and parameters provided in Tables 1,2 and 3 (for further details
126 on the assumptions in the “mizer” package see <https://sizespectrum.org/mizer/>).

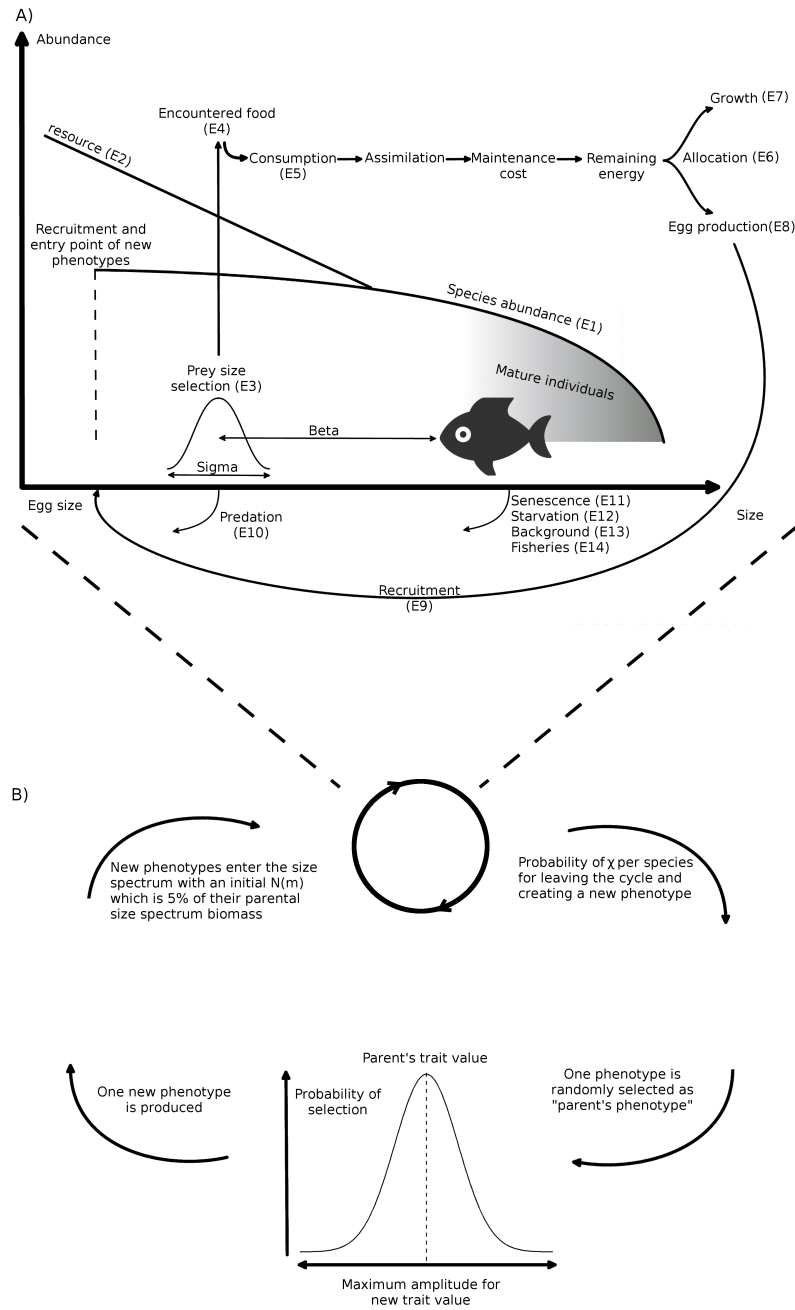


Figure 1: Schematic representation of key model components. A) shows the energy pathways occurring in the model through the different equations found in Table 2. E1, E2 and E9 govern the abundance of the different components. E3 to E5 are used for energy intake which is then divided between growth E7 and reproduction (E8) depending on the maturation state (E6). Mortalities are described by equations E10 to E14. B) shows the evolutionary processes built around the ecological model.

127 Ecological component

128 Size spectrum models are physiologically structured models that track the den-
129 sity of individuals at size through time ([Andersen, 2019](#)). The trait-based approach
130 means that the model has several “species” or size spectra, which differ only in their
131 asymptotic and maturation size (maturation size is assumed to be a fraction of
132 asymptotic size). This modelling approach has the desired combination of model
133 simplicity (only one set of physiological parameters required), but still allows for
134 multiple species with variable maturation sizes.

135 Growth, maturation and reproduction are all food-dependent, and driven by
136 the process of size-dependent predation, and the model therefore includes emergent
137 intra- and inter-specific competition. This means that the evolution in response
138 to fishing and predation is studied against a backdrop of underlying ecological
139 competition. Feeding, growth, mortality and reproduction occur at every time
140 step. The flux of individuals between size bins depends on growth (inflow from
141 smaller size bin, outflow to larger size bin) and mortality. The population dynamics
142 of each species is then obtained by solving the conservation equation ([McKendrick,](#)
143 [1926](#); [von Foerster, 1959](#)):

$$\frac{\partial N(m)}{\partial t} + \frac{\partial}{\partial m}(g(m)N(m)) = -\mu(m)N(m)$$

144 where m is the species mass and individual growth $g(m)$ and mortality $\mu(m)$
145 are determined by predation on/from other individuals, and a background resource
146 spectrum modelled using a semi-chemostat growth assumption (Table 2, [E2](#)).

147

148 *Food consumption*

149 In this model all individuals are simultaneously predators and prey, where no
 150 distinction is made between inter-specific predation and cannibalism. The available
 151 food comes from all of the fish species and a background resource size spectra,
 152 which here is assumed to extend from 10^{-10} to $1g$ (bacteria to zooplankton) (Table
 153 3, with the same regeneration rates as in [Hartvig et al. \(2011\)](#). All species begin
 154 life at the same size ($0.001g$) and compete for food in the resource size spectrum.
 155 As they grow larger the extent to which they feed on themselves and each other is
 156 dictated by a species interaction matrix and size-based feeding kernel. A species
 157 by species interaction matrix scales the proportion of available biomass of each
 158 prey species to each predator species, with the diagonal setting the intensity of
 159 cannibalism. Here we used two contrasting symmetric interaction matrices with
 160 all values set to either 0.5 or 0, depending on whether predatory interactions were
 161 included or not (see below). We chose 0.5 to define the predatory interactions,
 162 assuming that prey biomass is never completely available to predators at any given
 163 time, due to spatial or temporal separation and predator avoidance behaviour.
 164 When the interaction matrix is set to 0 all sizes and species compete for food in
 165 the resource size spectrum. Encountered food is the product of the volumetric
 166 search rate that scales with body size and the availability of food within the size
 167 spectrum ([Hartvig et al., 2011](#)).

168 Whether or not encountered prey are eaten is determined by a size-dependent
 169 feeding kernel with the preferred predator:prey mass ratio β and width of the
 170 feeding kernel σ (Table 3), and is described by a log-normal selection model:

$$\phi(m_p, m) = \exp\left[\frac{-(\ln(m/(\beta m_p)))^2}{2\sigma^2}\right]$$

171 where m_p is prey mass and m the predator mass.

172 Once the available size range has been determined, the realised food consump-
173 tion is modelled through a standard Holling type II functional response, determined
174 by the search rate and maximum intake rate, resulting in the emergent feeding (sa-
175 tiation) level (Table 2, E4 - E5).

176

177 *Growth*

178 The consumed food is assimilated with an efficiency α and the resultant energy
179 is divided between metabolism and growth (Table 2, E7), with the latter further
180 divided between somatic growth and reproduction (Table 2, E6) depending on the
181 maturation status. Resource allocation between growth and reproduction follows
182 a logistic curve, where half of the growth resources are allocated to reproduction
183 at maturation size, making fecundity scale with body size. We have modified E6
184 from Hartvig and Andersen (2013) and the 'mizer' default equation by changing
185 the scaling parameter (u , table 3) of energy allocation to reproduction from 10 to 7
186 to allow for a more prolonged period between minimum and maximum investment
187 in reproduction.

188

189 *Reproduction*

190 New recruits enter the smallest size class at every time step, i.e. the model
191 assumes continuous reproduction (Table 2, E8 and Table 3). Recruitment is de-
192 termined using the Beverton-Holt type stock recruitment relationship (Andersen
193 and Pedersen, 2010), defined by equation E9 (Table 2) and the maximum flux re-
194 cruitment parameter R_{max} (Table 1) (see below for further details on recruitment
195 in the evolutionary model). An upper limit on the recruitment flux (R_{max}) is used

to impose additional density-dependence otherwise not captured by the processes in the ecological model, but that are recognised to be important in marine fish populations (which also leads to an emergent stock-recruitment relationship; e.g. Andersen et al. 2016).

Mortality

In addition to the emergent predation mortality, other sources of mortality include senescence mortality (Table 2, introducing survival cost of reproduction, e.g. Kuparinen et al. (2012), E11), starvation mortality (Table 2, E12), a constant background mortality where larger species are assumed to have lower background mortality (Hartvig et al., 2011) (Table 2, E13), and fishing mortality (Table 2, E14).

Evolutionary Component

In this study we explore evolutionary changes in a single trait - maturation size. This was modelled through the η parameter, which defines the fraction of the theoretical asymptotic size at which 50% of an individual's net energy is allocated to reproduction (Table 3). We chose to modify η rather than asymptotic size (as in Zhang et al. 2015) to ensure that dynamic change in η only affects the resource allocation and the emergent growth, but not the background mortality which depends on theoretical asymptotic size (Table 2, E13). Changes in η through time were modelled similarly to the unstructured eco-evolutionary food web model of Allhoff et al. (2015) by introducing new size spectra ("phenotypes") characterized by new trait combinations. In contrast to Allhoff et al. (2015), however, who ran their simulation to equilibrium before adding new phenotypes (mutations) we

220 allowed for a possibility of new phenotypes to appear at each time step, assuming a
 221 constant influx of new mutations. Our approach assumes no interbreeding among
 222 phenotypes (new genetic variation is only generated via the mutation process),
 223 because each phenotype produces offspring identical to itself and no intermediate
 224 trait values among phenotypes emerge. This approach is also similar to that
 225 used in adaptive dynamics (Dieckmann and Law, 1996). As the simulations ran,
 226 each species generally had 10-50 phenotypes (Fig.S.10, showing the number of
 227 phenotypes per species through time), turning over their abundances through time
 228 in response to the selection forces at play. Our approach approximates temporal
 229 dynamics of η in response to selection by tracking each phenotype through time
 230 and computing the changing mean and variance of η for each species.

231 These new phenotypes were generated by randomly selecting an already exist-
 232 ing phenotype (i.e. set of parameter values) within a species to represent a “parent”.
 233 At each time step there is an equal probability that each species will generate a new
 234 phenotype. The new phenotype is a copy of its parent except for the maturation
 235 size for which values are randomly drawn from a normal distribution ranging from
 236 -20% to 20% of the parent’s trait value (Fig. 1). The initial abundance of the
 237 new phenotype was assumed to be 5% of the parent’s biomass, which is subtracted
 238 from the parent’s biomass. This means that phenotypes of less abundant parents
 239 have low initial abundance and lower chance to become established in a popula-
 240 tion, to ensure that the realized rate of evolution depends on the population size.
 241 Following their entrance into the ecosystem at egg size, the phenotypes compete
 242 for food and are predated upon, and hence change in abundance. The extinction
 243 threshold was set at $\Omega = 10^{-30} ind.m^{-3}$ (Hartvig et al., 2011) and all phenotypes
 244 below this density were removed. The probability of new phenotype appearance

245 χ was set to 0.001 per time-step and the initial η vales were assumed to be 0.25
 246 for all species (Hartvig and Andersen, 2013). This combination of parameters
 247 produced an expected evolutionary rate similar to that observed in populations
 248 with high fisheries intensity (Audzijonyte et al. 2013a, see Discussion). To en-
 249 sure robustness of these parameters for our findings, we explored the sensitivity
 250 of different values of χ and initial η along with other key parameters (Appendix 1).

251

252 *Balancing extinction and coexistence through food limitation*

253 We focus on the eco-evolutionary interactions between predation and fishing
 254 against the backdrop of food limited conditions, that includes inter- and intra-
 255 specific competition for resources. Food limitation is needed to enable some com-
 256 petition, extinction of less fit phenotypes, and temporal change in maturation size.
 257 The application of a maximum recruitment R_{max} assumes strong density depen-
 258 dence early in life; lower R_{max} leads to lower recruitment and reduces competition
 259 for a given resource density, while high R_{max} leads to competitive exclusion by
 260 one or a few species (Andersen et al., 2016). Because we are focussed on mod-
 261 elling evolutionary changes against the backdrop of food limitation, the initial
 262 R_{max} values were set for each species assuming the default values provided in the
 263 trait-based model of 'mizer' (see also Andersen 2019) and predation/resource pa-
 264 rameters were calibrated (σ , κ and r_0 , table 3) to ensure a balance of coexistence
 265 and food limitation (feeding levels between 0.12 and 0.7) (Table 1).

266 The phenotypes behave like separate species in that their size spectra are
 267 tracked independently and they compete with each other. However, all pheno-
 268 types in one species are affected by the same R_{max} . This means that during
 269 reproduction, all offspring are pooled within each species, one R_{max} applied to all

of them to calculate the new offspring numbers, and these are then distributed among phenotypes in proportion to their spawn output (i.e., a phenotype with a high spawn output will have more recruits with its traits than a phenotype with a low spawn output). Thus, abundant phenotypes are not disproportionately affected by R_{max} , which would be the case if it was applied to each phenotype separately.

Fitness calculations

As phenotypes are constantly being introduced and becoming extinct, the resulting fitness landscape and eco-evolutionary dynamics are ever-changing. We calculate fitness landscapes at several time intervals to explore the selection pressures on phenotypes through time.

We track the cohort survival and fecundity through time for 50 years (t_{max}), using a modified version of R_0 (lifetime reproductive output) as a proxy for fitness:

$$fitness = \frac{\int_{t_0}^{t_{max}} R_{max,i} \frac{R_{p,i}}{R_{p,i} + R_{max,i}} dt}{N_{p,i}(m_1, t_0)}$$

where $R_{p,i}$ is the energy allocated to reproduction (E8) by phenotype p of species i , $R_{max,i}$ is the maximum recruitment value for species i and $N_{p,i}(m_1, t_0)$ is the initial numbers of phenotype p and species i in the cohort of interest. This measure is similar to “eggs per recruit” (Andersen, 2019). We used this fitness calculation to construct snapshots of fitness gradients (in relation to maturation size) for all species’ phenotypes across all simulations to assess whether modelled directional changes are consistent with these gradients. Because different species have different R_{max} values, the fitness cannot be quantitatively compared across species, but they are comparable across phenotypes within a species where the

292 same R_{max} value applies.

293 **Simulation design**

294 To assess how predation affects evolution of species' maturation size under
295 fishing, we conducted simulations using four different model scenarios – with and
296 without fishing and with and without predatory interactions (interaction matrix set
297 to 0.5 or 0 respectively). In all simulations we used a model composed of 9 species
298 with asymptotic sizes equally spread on a logarithmic scale between 10 to $10^5 g$.
299 The initial abundance of each species was determined based on the equilibrium
300 conditions ([Andersen and Beyer, 2006](#)), which uses feeding and carrying capacity
301 parameters to estimate biomass at equilibrium (??). When predatory interactions
302 are disabled all species only feed on the background resource spectrum, but they
303 still compete for food.

304 Fishing was imposed through a knife-edge selectivity function, where all fish
305 at or above the selected size were subjected to an instantaneous fishing mortality
306 rate. For simplicity and to minimize the number of alternative fishing scenarios,
307 the selected size for all species is set at 0.25 of asymptotic size (i.e. at the ini-
308 tial maturation size). For the main set of scenarios, we applied the instantaneous
309 fishing mortality $F = 0.8 yr^{-1}$, as this was high enough to trigger ecological and
310 evolutionary responses, but sufficiently low to avoid extinctions, and represents
311 fishing pressure historically applied to many fish stocks (RAM Legacy Stock As-
312 sessment Database, [2020](#)). To assess the sensitivity of model outcomes to fishing
313 intensity we also explored the results with fishing mortality ranging from 0.1 to
314 1.0 per year.

315 Since the eco-evolutionary dynamics and fitness values change throughout the

Table 1: Initial maturation, asymptotic size and R_{max} of the species.

Species	Maturation size (g)	Asymptotic size (g)	R_{max}
1	2.5	10	0.49208
2	8	32	0.19854
3	25	100	0.08011
4	79	316	0.03232
5	250	1000	0.01304
6	790	3162	0.00526
7	2500	10000	0.00212
8	7905	31622	0.00085
9	25000	100000	0.00034

simulations as new phenotypes appear, the model is not necessarily expected to reach equilibrium conditions. To account for stochasticity of the eco-evolutionary dynamics, each scenario (parameter combination) was repeated 10 times. To test whether 10 stochastic realisations were enough to capture trends, we also ran all predation-enabled scenarios with 50 replicates but found no substantial difference in trait changes and variances (See Fig.S.7 and S.8 in Appendix 1).

The simulations were run for 3000 years without fishing to allow the ecosystem to build up multiple phenotypes per species, establish evolutionary trends in the absence of fishing and for the influence of initial conditions to dissipate. After 3000 years, the full simulation state of each stochastic run was saved and used to initiate two additional 3000 years of simulations, with and without fishing imposed. The effects of fishing on the evolutionary dynamics were assessed by comparing dynamics and final states in simulations with and without fishing.

The sensitivity of the model outcomes to the parameter values was assessed across a range of: fishing mortalities (0.1 to 1); the initial trait value η (Fig.S.1); the standard deviation between parent and new trait (Fig.S.2); new phenotype

332 appearance rate χ (Fig.S.3); the initial phenotype abundance (Fig.S.4); width of
333 the feeding kernel σ (Fig.S.5); and preferred predator-prey mass ratio β (Fig.S.6).

334 Analyses of simulation outputs

335 We assessed the modelled communities by exploring phenotypes' abundance
336 history (i.e., phenotype biomass time series including when they appear and go
337 extinct) and evolutionary trends of each species' average relative maturation size η .
338 This was calculated as the abundance weighted mean trait value across all pheno-
339 types for each species in each simulation through time. Since the simulations were
340 conducted as a factorial design (predation x fisheries) we tested whether final values
341 of η (after 6000 years) depended on the interaction of Species*Predation*Fishing
342 using a three-way Model 1 (fixed effects) ANOVA, where Predation (0 or 1), Fish-
343 ing (0 or 1) indicate presence or absence of predation and Species is the species
344 number, with $n = 10$ replicate simulations. To ensure among-group homogeneity of
345 variance in residuals we log-transformed η (after transformation the homogeneity
346 was achieved).

347 All three terms and their interactions were evaluated using F-tests and model
348 comparisons were carried out using delta AIC tests. While we report p-values, the
349 purpose of these models was to evaluate and interpret the nature of the interactions
350 in the model. Statistics were done using R version 4.0.0 (R Core Team, 2020), the
351 'effects' (v4.1-4; Fox et al., 2019) and the 'emmeans' (v1.4.7; Lenth et al., 2020)
352 packages. The lower and upper 95% confidence intervals for all model predicted
353 effects were calculated using the allEffects function in the R package 'effects'.

354 To assess whether the final values of maturation size (η) were compatible with
355 empirical observations, we compared our results with empirical estimates for wild

356 fish stocks (Rijnsdorp et al., 1992; Reznick et al., 1997; Jennings et al., 1998;
357 Conover and Munch, 2002; Goodwin et al., 2006; Ulloa et al., 2011; Olsson and
358 Gislason, 2016).

359 Results

360 Maturation size trajectories

361 During the initial 3000 years of simulations without fishing, the presence of
362 inter- and intra-specific predation had large effects on the evolution of maturation
363 sizes (Fig.2). In simulations without predation the relative size at maturation
364 decreased substantially (40 – 90%) in all but the largest two species (Fig.2b, before
365 the dashed line). In contrast, when predation was enabled the evolution of
366 maturation size diverged across the three size groups, where the smallest three
367 species evolved towards smaller maturation (decrease by 45 – 60%), the middle
368 sizes species towards larger maturation size (increase by 50 – 150%), and in the
369 largest three species the trait evolved slightly in either direction (Fig.2d, before
370 the dashed line). After the initial 3000 years, the trend of evolution in scenarios
371 without fishing generally continued in the same direction at a slower rate or stabilised
372 for the remaining 3000 years (difference between the dashed line and solid
373 line in Fig.2b and d).

374 After the introduction of fishing at year 3000, the biomass of many species
375 quickly reached a lower state (Fig.2a-c dashed lines), but then recovered in some
376 species as they evolved to adapt to new mortality regimes. In all species and
377 scenarios, fishing led to either decreasing or static maturation size, the latter
378 mostly occurring in cases where maturation size has already evolved to be less

379 than 50% the starting value (except species 5 with predation, Fig.2d). For the
 380 entire ecosystem, the decline in maturation size due to fishing was stronger when
 381 predatory interactions were enabled compared to simulations without predation
 382 (strong decrease in maturation size for 5 out of 9 versus 2 out of 9 species in the
 383 community, Fig.2b-d), suggesting that fishing had a large effect on the ecosystem
 384 with predation. Our statistical analyses of the model simulations showed that
 385 the effect of fishing (red dots in Fig.3) reduced maturation size in medium and
 386 large species. All terms of the model were significant (Table S.2) and there was a
 387 significant three-way interaction among species, predation and fishing (ANOVA:
 388 $F = 2.6$, $df = 8.324$, $p = 0.009$). The differences between maturation size between
 389 fished and unfished simulations clearly depended on the species and whether or
 390 not predation was enabled. Significantly lower maturation sizes in the presence of
 391 fishing were found for species 4,8, and 9 without predation (pairwise comparison
 392 tests, $p < 0.005$) and 4,6,7,8, and 9 with predation (pairwise comparison tests,
 393 $p < 0.001$). Across stochastic realisations of simulations, variation in the final
 394 maturation size values was generally small for all species when predation was dis-
 395 abled, especially when variation is considered as a proportion of the η (i.e. species
 396 with larger η have larger absolute variations in Fig.3, but the proportional varia-
 397 tion is similar). With predation enabled, variation was small in the three smallest
 398 species, and very large in the two medium sized species (species 4 and 5) (Fig.3).
 399 Sensitivity analyses showed that the observed impacts of fishing were qualitatively
 400 similar across a range of tested parameter values (see Appendix 1).

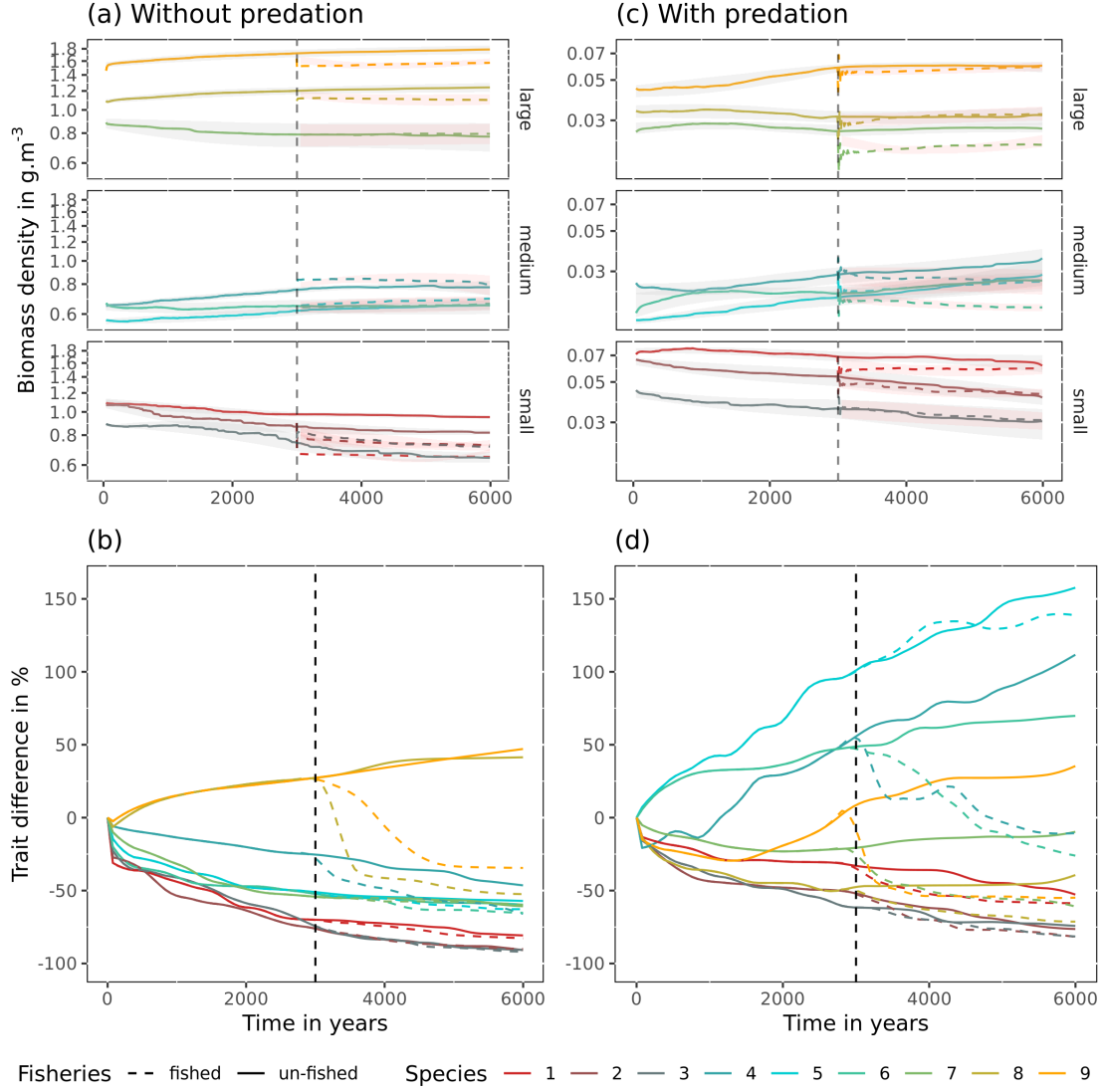


Figure 2: Biomass and trait variation averaged and smoothed throughout all simulations in scenarios without predation (a-b) and with predation (c-d). (a,c) is the change in species' biomass, the grey shading indicates the standard deviation across simulations. (a,c) is divided in 3 panels (small, medium, large being the species asymptotic size) for more clarity. The vertical line shows the introduction of fishing and from this line, the dashed lines are the biomass when fished, with the red shading showing its standard deviation. (b,d) is the proportional change in weighted mean maturation size for each species relative to its initial value averaged across all stochastic realisations. The vertical line shows the time where fishing is introduced, and the dashed line shows simulations with fisheries.

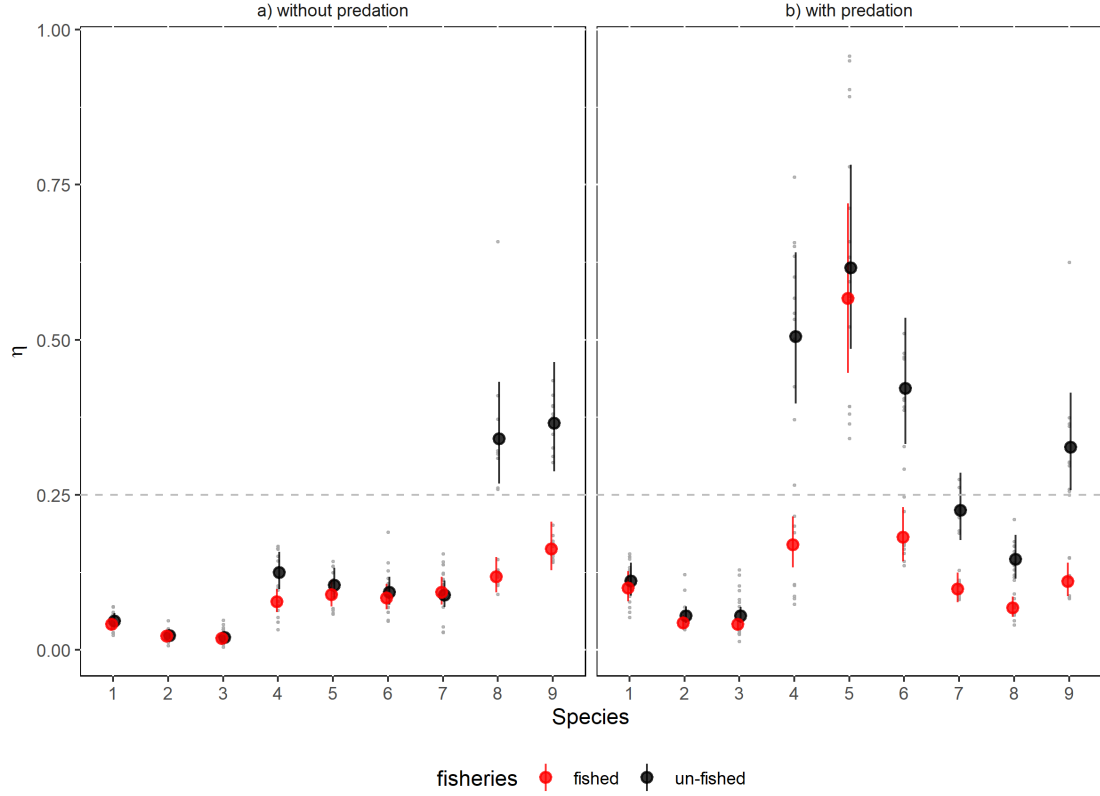


Figure 3: Final maturation size (relative to each species' asymptotic size) (η) at the end of the simulation (6000 years). Each dot shows the predicted means and 95% confidence intervals from the 3-way ANOVA model for each species, predation and fisheries combination. Data points show weighted average η for each species (across 10-50 phenotypes, see Fig.S.10 for the number of phenotypes per species) where each light grey point is a replicated simulation (10 simulations for each combination of fisheries and predation scenarios). The dashed line indicates the initial relative maturation size value (η).

401 **Maturation size changes in relation to fitness gradients**

402 The species-specific maturation sizes responses to fishing and predation can be
403 in part understood by examining their fitness gradients at a given time (Fig.4 shows
404 these at the onset of fishing in year 3000, and Fig.S.9 shows them close to the end
405 of the simulation period). For the smallest species neither predation nor fishing
406 had much effect on the fitness gradient, where phenotypes with smaller maturation
407 sizes had slightly higher fitness values, explaining the observed constant and slow
408 evolution towards smaller maturation size. Introduction of fishing generally did
409 not alter the shape of the fitness gradients for these species (red dots compared
410 to the black dots, Fig.4, top three rows). In contrast, the medium-sized species'
411 response to fishing strongly depended on whether or not predation was enabled.
412 When predation was disabled, smaller maturation sizes of medium-sized species
413 had higher fitness (Fig.4 centre three rows, left panels), explaining their evolution
414 towards smaller body sizes (Fig.3 no predation panel) whereas the opposite was
415 generally true when predation was enabled (except in species 4, where the fitness
416 gradient was not monotonic and either the smallest or largest maturation sizes had
417 the highest fitness). Introduction of fisheries only steepened the fitness gradients
418 in scenarios without predation (both in year 3000 and year 5500, Fig.S.9), making
419 smaller maturation sizes even better adapted while for scenarios with predation
420 the effect of fishing on fitness landscapes was less defined, with large variation
421 across phenotypes (the difference in fitness gradients was more clear for species
422 6). This response can explain the large variation in the evolutionary trends across
423 stochastic simulations for species 4 and 5 (Fig.2d), suggesting that eco-evolutionary
424 dynamics may be less predictable for the medium-sized species because of the

425 interplay of selection pressures from fishing and predation. Finally, the effect of
426 fishing was especially clear on the fitness gradients of the largest species, where
427 smaller maturation sizes always had higher fitness under fishing, and phenotypes
428 with large maturation sizes were largely absent after 2500 years of fishing (Fig.4
429 and [S.9](#)).

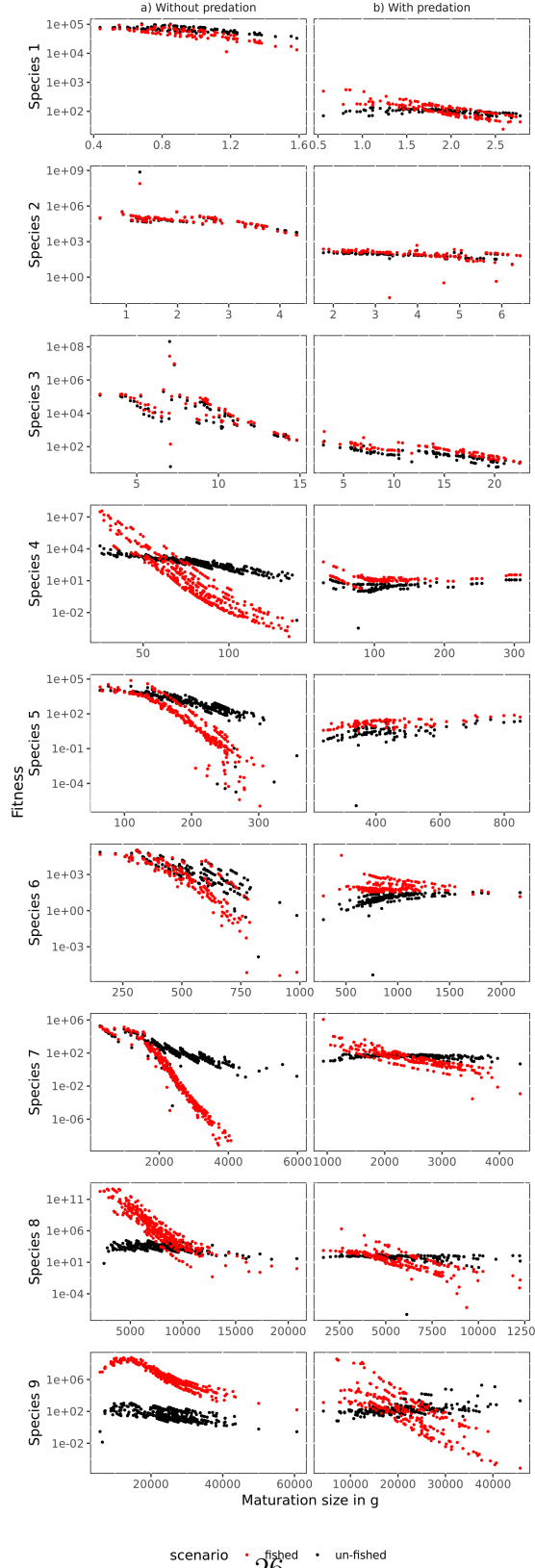


Figure 4: Species' fitness across simulations. Each dot shows fitness of a phenotype with different maturation size in scenarios with (red) and without (black) fishing across simulations. The figure shows phenotypes in a cohort starting at year 3001 in simulations without (a) and with (b) predation, following the introduction of fisheries. Fitness landscapes in year 5500 were generally similar and shown in Fig.S.9

Impact of increasing fisheries effort

We explored how changes in the intensity of fishing affected trait evolution, by repeating simulations with predation for ten values of instantaneous fishing mortality rate – from 0 to $1yr^{-1}$. For the largest four species (species 6-9) the only level of fishing mortality that did not lead to strong decrease in maturation size was $0.1yr^{-1}$. Increasing fishing mortality to $0.2yr^{-1}$ caused maturation size to decline. Indeed maturation size stayed relatively stable at this new level for all mortality values above $0.4yr^{-1}$ ($0.7yr^{-1}$ for species 6) (Fig.5). For the three smallest species changes in fishing mortality did not have much effect, because their maturation size was close to the smallest possible given the physiological trade-offs assumed in the model (i.e. reproductive output is size dependent, so at least some growth is needed for reproduction to occur) and the computational constraints of the model where the maturation size was reached in just a few time-steps. Finally, two of the medium-sized species (species 4 and 5) had large variance in their maturation sizes. For species 5, where fishing did not significantly reduce the maturation size, increasing fishing effort also did not have a clear effect. For species 4, clear effects of fishing on maturation size were seen only at high fishing mortalities ($F \geq 0.8yr^{-1}$).

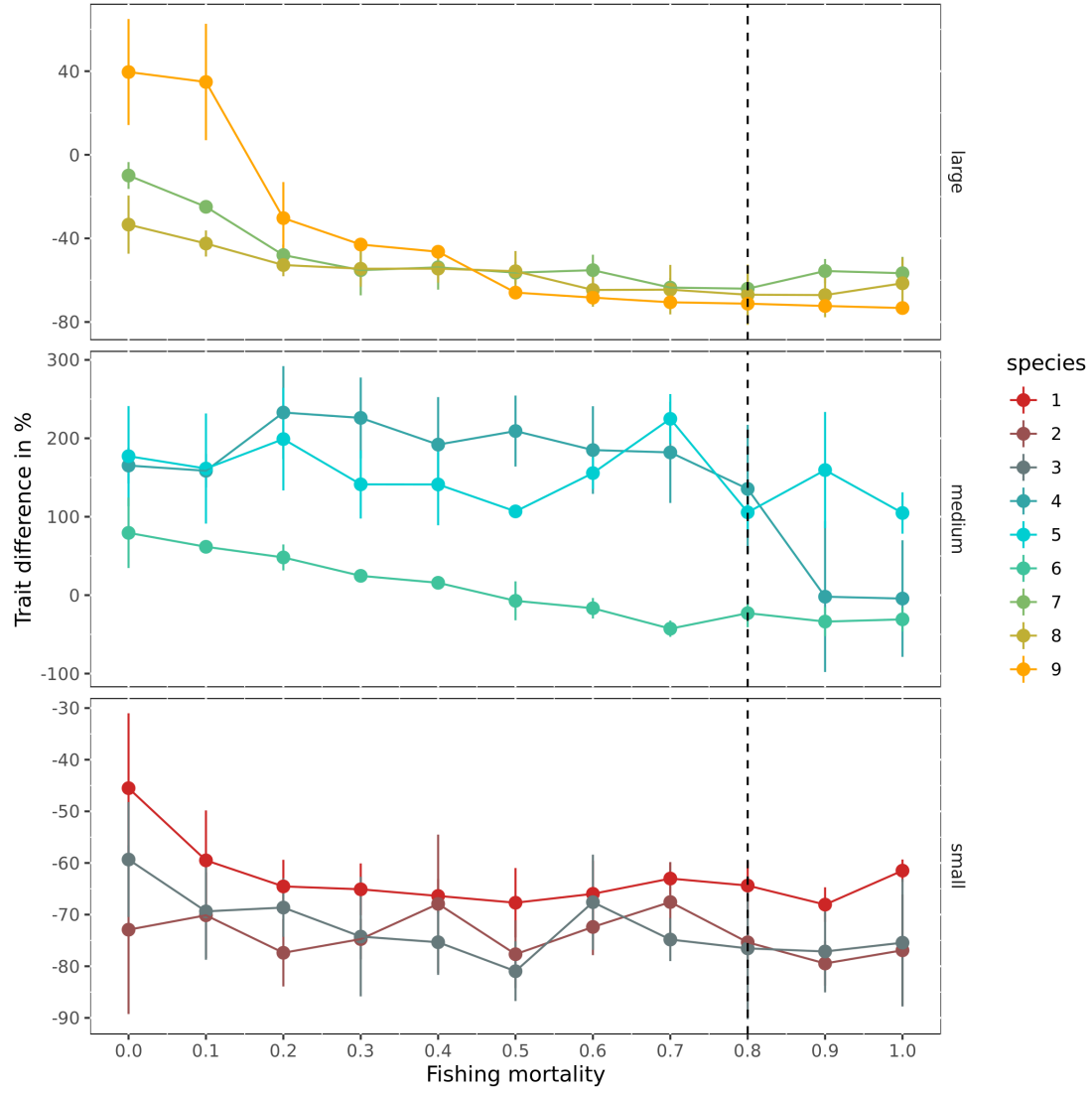


Figure 5: The effect of the instantaneous fishing mortality rate (yr^{-1}) on changes in maturation size in scenarios with predation. Each line shows the biomass weighted average trait value at the end of the simulation for each species. Error bars show the standard deviation across simulations. The vertical dashed line shows the default parameter values used in the study.

448 **Comparison with empirical patterns**

449 We found that despite divergent evolution of maturation sizes the emergent
450 relationship between the maturation size and maximum body size (at year 6000)
451 generally fell within the range of empirical relationship observed for marine fish
452 across a range of body sizes (Fig.6). The overall slope of this relationship remained
453 consistent across simulations with and without fishing.

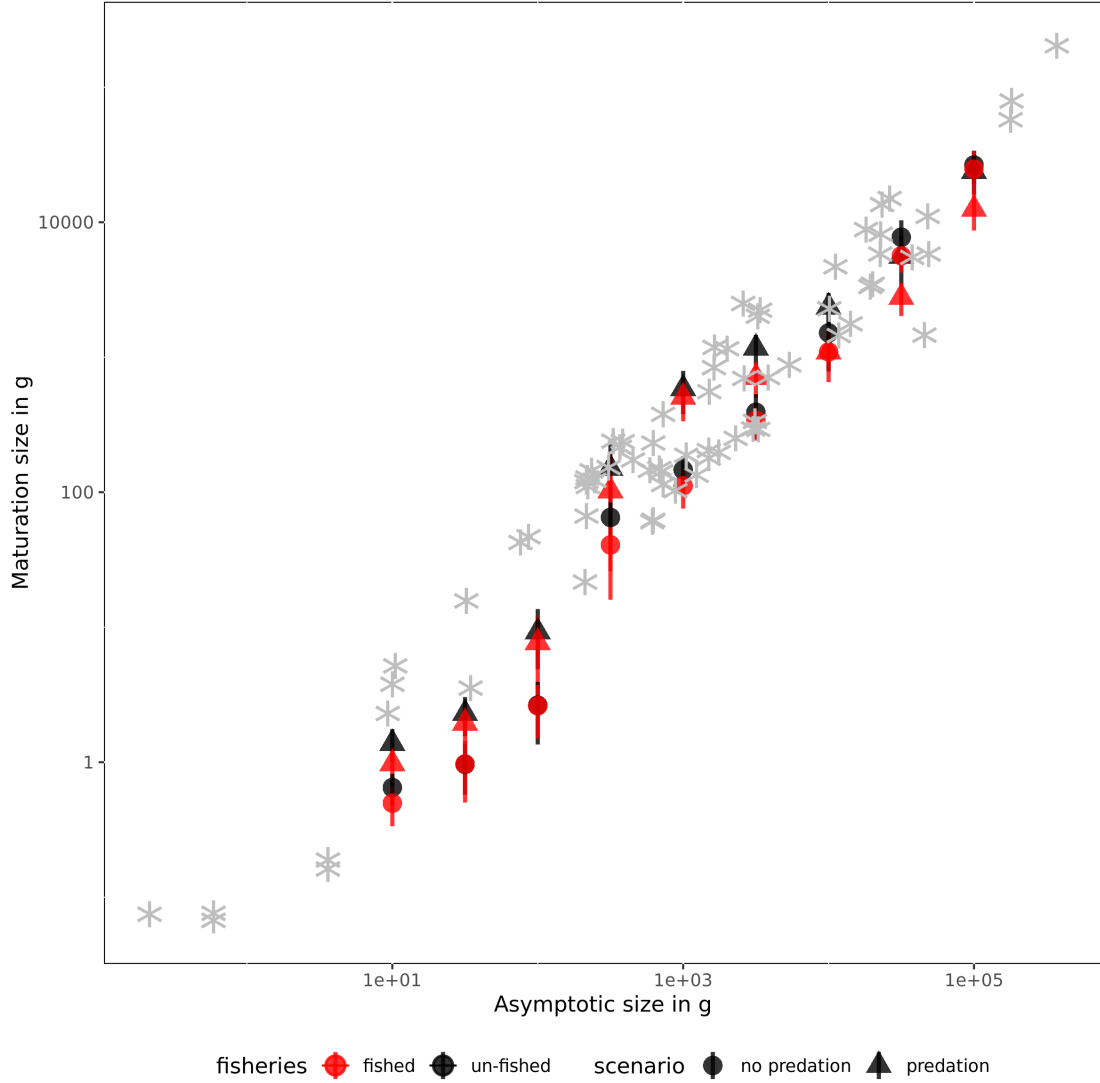


Figure 6: Modelled and empirical relationship between maturation size and asymptotic size. Modelled estimates of maturation size are from the end of the simulation period (year 6000) with (red) and without (black) fishing and with (triangle) and without (circle) predation. Error bars show the standard deviation across simulations. Silver asterisks are values obtained from empirical studies of fish species for comparison (see table S.3 for data and references).

Discussion

The eco-evolutionary model presented here aims to tackle the interplay between predatory interactions and size dependent fishing on the evolution of maturation size. The model uses simple rules of size-dependent predation, body size scaling of physiological processes, and introduction of random trait variation. There are four key findings of this study. First, we show that without any constraints on the direction and limits of maturation size, substantial changes in the evolutionary trends in maturation size emerge, but these changes are broadly consistent with empirically observed patterns. Second, we show that both predation and fishing are strong selective forces, but their effects interact and differ across species of different asymptotic sizes. For the small species, regardless of predation and fishing, species evolved towards smaller maturation sizes. In contrast, predation completely reversed selection gradients in the medium sized species, while fishing generally reversed selection and trait evolution in medium and large species. Third, in agreement with single-species predictions, fisheries generally led to smaller maturation sizes for all but the smallest three species, and its effects were stronger in ecosystems with predation (and cannibalism) enabled. Fourth, for the largest species even low fishing mortality ($0.1yr^{-1}$) was enough to drive evolutionary change toward smaller maturation size, as predation mortality was considerably lower than fisheries mortality at the largest sizes.

Predation and emergent maturation size

The role of predation on optimal maturation size has been addressed in a range of models, including size spectrum approaches, generally suggesting that matura-

tion sizes diverge to promote species co-existence (de Roos et al., 2006; Hartvig and Andersen, 2013; Allhoff et al., 2015; Zhang et al., 2015). However, these studies used an adaptive dynamics approach and assessed optimal fitness or invasion success of new traits in equilibrium conditions, separating ecological and evolutionary time scales. While the findings of these studies are important, they did not include continuous ecological-evolutionary feedbacks known to shape natural systems (Govaert et al., 2019). Evolutionary feedbacks of species in a multi-species system have previously been suggested to be equally important driver of community response as harvesting (Wood et al., 2018). This is consistent with our findings, which demonstrated that in a number of species the maturation size trajectories varied substantially through time and across stochastic realisations, even when biomass was relatively stable through time. This suggests that the timing and ecological conditions present at the time phenotypes emerged can greatly affect their success, particularly within medium-sized species.

Despite the variation across stochastic realisations and temporal dynamics in trait values, one of the most consistent evolutionary trends seen in our study is the decreasing maturation size of the smallest species in all scenarios, irrespective of predation or fishing. This is illustrated by similar fitness trends across the scenarios (i.e. smallest maturation sizes had higher fitness for small species in all four scenarios of predation and fishing) and could partly be explained by the food limitation at around $10g$ (seen as a drop in feeding level, see Fig.S.11). By evolving towards smaller maturation size, species divert fewer resources to growth, can stay longer in size groups between 1 and $10g$, benefit from better feeding conditions, but are not yet exposed to high predation (see panel b in Fig.S.11). Thus, trends in maturation size strongly depend on the resource availability, which is consistent

502 with [Hartvig and Andersen \(2013\)](#), where optimal maturation and asymptotic
503 sizes in a single- or two-species size spectrum models was entirely determined by
504 the resource density. Moreover, [Hartvig and Andersen \(2013\)](#) showed that the
505 system can exist in different stable states depending on whether feeding limitation
506 occurred at an early juvenile stage or around the maturation size (see [Claessen
507 and de Roos 2003](#), for a similar finding in an age-structured model). This means
508 that some combinations of size-specific resource limitation and maturation size are
509 unstable and will select for either smaller or larger maturation size.

510 The key difference between [Hartvig and Andersen \(2013\)](#) and our study de-
511 sign is that the former explored the evolution of asymptotic size, while always
512 setting the maturation size to be a fixed proportion of the asymptotic size. Yet,
513 asymptotic size also determined background mortality (which can be high in small
514 species) and the final evolutionary drivers (competition, predation or differences
515 in background mortality) were hard to identify. The factorial design of our simula-
516 tions aimed to tease apart some of these drivers. Also, by specifically allowing for
517 evolution of the η parameter, we allow the maturation size to evolve independently
518 of the asymptotic size without affecting the background mortality. Additionally,
519 we introduced the survival cost of reproduction (small increase in mortality af-
520 ter maturation), which are ubiquitous in nature and have an effect on evolution
521 of maturation size ([Kuparinen et al., 2012](#)). In our design the asymptotic size
522 becomes a more theoretical parameter setting the largest possible body size. In
523 reality, as maturation size, growth rates, and mortality evolve and change through
524 time, many species never reach their asymptotic sizes. Nevertheless, both our and
525 [Hartvig and Andersen \(2013\)](#) study share the same general finding – food limita-
526 tion at around the maturation size will act as a strong selective force (for small

species in our study).

Another notable finding is the evolution of maturation size in medium sized species, where predation reverses the maturation size trends and leads to a rapid increase rather than decrease in maturation size seen in scenarios without predation. Together with large variation in maturation sizes in middle sized species this suggest that alternative maturation strategies might exist for these species, all dependent on the dynamic size specific mortality from predation and fishing. Although we did not study alternative stable states, our findings are consistent with e.g. [Gårdmark and Dieckmann \(2006\)](#) showing that such alternative stable solutions do indeed exist. As in [Gårdmark and Dieckmann \(2006\)](#), an important trade-off in our model is the divestment of resources from growth to reproduction at around the maturation size. Delayed maturation size means that more energy at smaller size is available for growth and individuals will move faster to larger size classes, where they can potentially escape predation. The advantage of earlier or delayed maturation will therefore critically depend on the size at which predation mortality is lowest and feeding levels are highest (see also [Pope et al. 1994](#); [Duplisea 2005](#)).

Fishing and emergent maturation size

The response of maturation size to fishing has been studied using a range of size and age-structured single-species models ([de Roos et al., 2006](#); [Andersen et al., 2007](#); [Enberg et al., 2009](#)). Generally, these studies show that increased mortality due to fishing selects for earlier or smaller maturation size. For example, for the Baltic Sea cod (*Gadus morhua*) the optimal maturation size was predicted (based on single-species and sized structured deterministic model) to be at least

10 times smaller than currently observed ([Andersen et al., 2007](#)). Yet, selection in wild populations is a tug of war among predation, pathogenic, competition, sexual selection and human pressures ([Edeline et al., 2007](#); [Carlson et al., 2007](#); [Darimont et al., 2007](#)). For fish in particular, predation is a powerful force, imposing strong selection on size, especially early in life ([Perez and Munch, 2010](#)), but also in adult individuals ([Olsen and Moland, 2011](#)). The strength of predation (including cannibalism) can counteract or even reverse evolutionary effects of fishing, such as in Lake Windermere pike *Esox lucius* ([Edeline et al., 2007](#)). It is therefore unclear how often and for which species harvest induced selection might be strong enough to override selection from predation or competition (e.g. [Edeline et al. 2007](#); [Kuparinen and Merilä 2007](#); [Eikeset et al. 2016](#)).

Our results suggest that if predation is strong in early life stages and delayed maturation can help to outgrow this window, evolutionary effects of fishing can be particularly strong, as in some middle sized species (species 4 and 6). However, due to this predation versus fishing “tug of war” evolutionary impacts of fishing are not manifested until fishing mortality becomes relatively high (in species 4). Nevertheless, in one middle sized species (species 5) fishing did not reduce maturation size, as selection from predation, and possibly slightly improved food availability at slightly larger sizes (Fig.S.11) outweigh the selection from fishing. While this may look like good news, such species might be particularly vulnerable to long-term exploitation, unable to improve their fitness by evolving towards earlier maturation.

For large bodied species the effect of fishing followed our expectations. In agreement with observations that harvesting imposes very strong selective pressures (e.g. [Wood et al. 2018](#)), fishing completely reversed natural selection gradients (in more

realistic simulations with predation enabled) and led to a rapid evolutionary re-
 sponse of maturation size. The actual rate of response in our simulations cannot
 really be compared to real world ecosystems, because generation time, levels of
 phenotypic diversity and the genetic inheritance mechanisms in the model, do not
 accurately represent those in real fish populations. Nevertheless, the fastest rates
 of change observed in our model are broadly compatible with rates of change in
 empirically observed fish stocks or those predicted in ecogenetic models with more
 accurate evolutionary mechanism. The fastest rates observed in our simulations
 occur after the introduction of fishing, and are in the range of 50% in 300 years
 or 0.17% per year (Fig. 2b-d). In intensively fished stocks (F values similar to our
 baseline simulations) observed rates of phenotypic change are 1% per year, but
 this rate is likely to include both evolutionary and plastic trends. The rate (1%
 per year) is about four times faster than evolutionary rates reported in various
 population and ecogenetic models (Audzijonyte et al., 2013b), which is also com-
 patible with our findings. The important result is that the evolutionary response
 occurred even at the instantaneous fishing mortality of $0.1yr^{-1}$, which is generally
 considered a low level of fishing mortality, below levels that are consistent with
 maximum sustainable yield (Blanchard et al. 2014, www.ices.dk). This finding is
 consistent with other evolutionary models demonstrating that even low levels of
 fishing will select for smaller maturation size (e.g. Andersen et al. 2007).

Model limitations and future work

Although this study and modelling exercise is seemingly complex, it is a sub-
 stantial simplification of real marine ecosystems. The fishing scenarios explored
 target all species with similar size selectivity and intensity and were stable through

600 time. The initial set of species was spaced evenly over size categories and had
 601 shared diet preferences and other physiological parameters. None of this is true
 602 in the real world. We used an initial maturation size value of a quarter of the
 603 asymptotic size ([Andersen and Pedersen, 2010](#); [Hartvig et al., 2011](#)) but different
 604 and even multiple optima may exist for species of different sizes. The evolutionary
 605 mechanism itself is highly simplified and does not include trait recombination or
 606 covariances, and each phenotype only produces offspring identical to itself. This
 607 means that selection differentials from the model cannot be compared to empirical
 608 studies. Finally, even though we included survival cost of reproduction, the full
 609 set of reproductive costs may still be too small. This could explain very small
 610 evolved maturation sizes in species – if a threshold amount of energy is required
 611 to achieve maturation, it would set a limit on how small maturation size could
 612 be. Indeed, a model with energetic cost of reproduction included ([Audzijonyte
 613 and Richards, 2018](#)) predicted a more realistic and larger maturation size of in-
 614 tensively fished Baltic Sea cod than a model without such costs ([Andersen et al.,
 615 2007](#)). Yet, despite these simplifying assumptions, we found a general emergent
 616 pattern of a conserved ratio of maturation sizes and maximum sizes that was con-
 617 sistent with empirical values (Fig.6). Our observed evolutionary rates were also
 618 broadly compatible with those expected in wild stocks. The range of η values from
 619 our model fell within the empirical range, noting that those values were obtained
 620 from species' maturation weight and weight at infinity from empirical von Berta-
 621 lanffy relationships. Future studies would be worthwhile to further assess whether
 622 the predicted changes and timescales involved would still hold under more realistic
 623 species composition, traits, diets, and more realistic fishing scenarios.

Conclusion

One of the key questions in our study was to assess whether predation-driven selection could counteract or even reverse fishing induced evolution (FIE). In this size and trait-based food-web model, the answer is that this is generally not the case, although it depends on the size of the species considered and fishing intensity imposed. Our findings suggest that for the largest species, harvesting, even at low intensity, imposes very strong selection because they have low predation mortality at around and above their maturation size. In contrast, the smallest species may be mostly limited by food availability, and neither predation nor fishing affect their fitness landscapes substantially. Such species may be already maturing close to their physiological or ecological limit, especially if cost of reproduction is considered (e.g. [Audzijonyte and Richards 2018](#)). This shows the importance of simultaneously considering bottom up processes (e.g. food availability) when looking at FIE, and highlights the benefits of physiologically structured multi-species models where growth and reproduction are dependent on food availability. Finally, the most unpredictable eco-evolutionary responses emerge in medium sized species, sandwiched between larger predators and smaller competitors. For these species, selection pressures from fishing, predation and competition fluctuate through time and here predation release may indeed occasionally balance the selection from fishing. These findings call for more empirical studies on the possible evolutionary trends in medium sized species, improved understanding of interactive forces of selection, and stronger precautionary measures to minimise FIE in large fish.

646 Authors' Contributions

647 RF, JLB and AA conceived the ideas, designed methodology, and led the writ-
648 ing of the manuscript; RF collected and analysed the data. All authors contributed
649 critically to the development of the study, drafts and gave final approval for pub-
650 lication.

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657 Data accessibility

658 All data and model open source code are available on <https://github.com/baldrech/MizerEvo>.

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857 terference competition and their impacts on the ecology and evolution of size-
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Tables

Table 2: Model equations for each species' ecological dynamics. Subscripts for each species are not included in the equations below for readability. These dynamics also hold for each phenotype (nested within each species) once they have entered the size spectrum. Equation numbers reference the processes illustrated in Figure 1 and descriptions in main text. $N(m)$ is the density at size driven by: $g(m)$ which is the feeding dependent growth rate at size and $\mu(m)$ which is the mortality at size, the latter is comprised of several mortality terms below. All parameter values and definitions are provided in Table 3 or the main text.

Equation	Description	
Species population dynamics	$\frac{\partial N(m)}{\partial t} + \frac{\partial}{\partial m}(g(m)N(m)) = -\mu(m)N(m)$	(E1)
Background resource dynamics	$\frac{\partial N_R(m, t)}{\partial t} = r_0 m^{p-1} [\kappa_R m^{-\lambda} - N_R(m, t)] - \mu_p(m)N_R(m, t)$	(E2)
Prey size selection by size m predator	$\phi(m, m_p) = \exp\left[\frac{-(\ln(m/(\beta m_p)))^2}{2\sigma^2}\right]$	(E3)
Encountered food by size m predator across all sizes (m_p) of species j prey	$E(m) = \gamma m^q \int \left(N_R(m_p) + \sum_j \theta_j N(m_p) \right) \phi(m, m_p) m_p dm_p$	(E4)
Feeding level	$f(m) = \frac{E(m)}{E(m) + hm^n}$	(E5)
Energy allocation towards reproduction	$\psi(m) = \left[1 + \left(\frac{m}{m^*} \right)^{-u} \right]^{-1} \left(\frac{m}{M} \right)^{1-n}$	(E6)

Somatic growth	$g(m) = (\alpha f(m)hm^n - k_sm^p)(1 - \psi(m))$	(E7)
Reproduction	$R_p = \frac{\epsilon}{2m_0} \int N(m)(\alpha f(m)hm^n - k_sm^p)\psi(m)dm$	(E8)
Recruitment	$R = R_{max} \frac{R_p}{R_p + R_{max}}$	(E9)
Predation mortality on size mp prey inflicted by all sizes (m) of species j predators	$\mu_p(m_p) = \sum_j \int \phi(m, m_p)(1 - f_j(m))\gamma_j m^q \theta_j N_j(m)dm$	(E10)
Senescence mortality	$\mu_{se} = \begin{cases} se_{min} + (se_{max} - se_{min})e^{-\frac{M}{m}}, & \text{if } m > m^* \\ 0, & \text{otherwise} \end{cases}$	(E11)
Starvation mortality	$\mu_{st} = \begin{cases} st_r m \left(k_sm^p - \alpha f(m)hm^n \right), & \text{if } k_sm^p > \alpha f(m)hm^n \\ 0, & \text{otherwise} \end{cases}$	(E12)
Background mortality	$\mu_b = \mu_0 M^{n-1}$	(E13)
Fishing mortality	$\mu_f = \begin{cases} 0.8, & \text{if } m \geq m^* \\ 0, & \text{otherwise} \end{cases}$	(E14)

Table 3: Parameters table. M is noted "variable" as it is species specific (values in Table 1). η starts at 0.25 for all species but will evolve during the simulations. Parameters values are taken from Hartvig et al (2011). The value from γ was calculated from: $\gamma = h \frac{f_0}{\sqrt{(2\pi)\sigma\beta\lambda^{-2}e^{((\lambda-2)^2\sigma^2/2)}\kappa(1-f_0)}}$ (Hartvig et al., 2011). Initial values for the abundance density $N(m)$ of each species at $t = 0$ were based on the equilibrium equation: $N = \frac{\kappa}{1000} M^{(2n-q-2+0.35)} m^{(-n-0.35)}$ provided in Andersen and Beyer (2006).

Symbol	Value	Units	Parameter
Individual growth			
M	variable	g	Asymptotic size
η	0.25	-	ratio between M and m^*
m^*	ηM	g	Maturation size
f_0	0.5	-	Initial feeding level
γ	538	$g^{-q}m^3yr^{-1}$	Factor for search volume
α	0.6	-	Assimilation efficiency
h	85	$g^{1-n}year^{-1}$	Maximum food intake
n	0.75	-	Exponent for max. food intake
p	0.75	-	Exponent for standard metabolism
ks	4	-	Factor for standard metabolism
β	100	-	Preferred predator-prey mass ratio
σ	1	-	Width of the feeding kernel
q	0.8	-	Exponent of search volume
Reproduction			
m_0	0.1	mg	Offspring mass
ϵ	1	-	Efficiency of offspring production
u	7	-	Width of maturation transition
Mortality			
ξ	0.1	-	Fraction of energy reserves
μ_0	2	$g^{1-n}year^{-1}$	Background mortality
se_{max}	1	$g^{1-n}year^{-1}$	Upper limit for senescence mortality
se_{min}	0.1	$g^{1-n}year^{-1}$	Lower limit for senescence mortality
st_r	0.1	$year^{-1}$	Starvation mortality cost
θ	variable	-	Interaction matrix species-specific value
Resource spectrum			
κ	0.05	$g^{\lambda-1}m^{-3}$	Magnitude of resource spectrum
λ	$2 - n + q$	-	Slope of resource spectrum
r_0	4	$g^{1-p}year^{-1}$	Regeneration rate of resources
m_{cut}	1	g	Upper limit of resources spectrum
Evolution			
χ	0.001	-	Phenotype's introduction probability
Ω	10^{-30}	$individual/m^3$	Extinction threshold
	5%	-	Fraction of initial phenotype's abundance
	+ - 20%	-	Magnitude of trait evolution

Appendices

Appendix1: sensitivity analysis

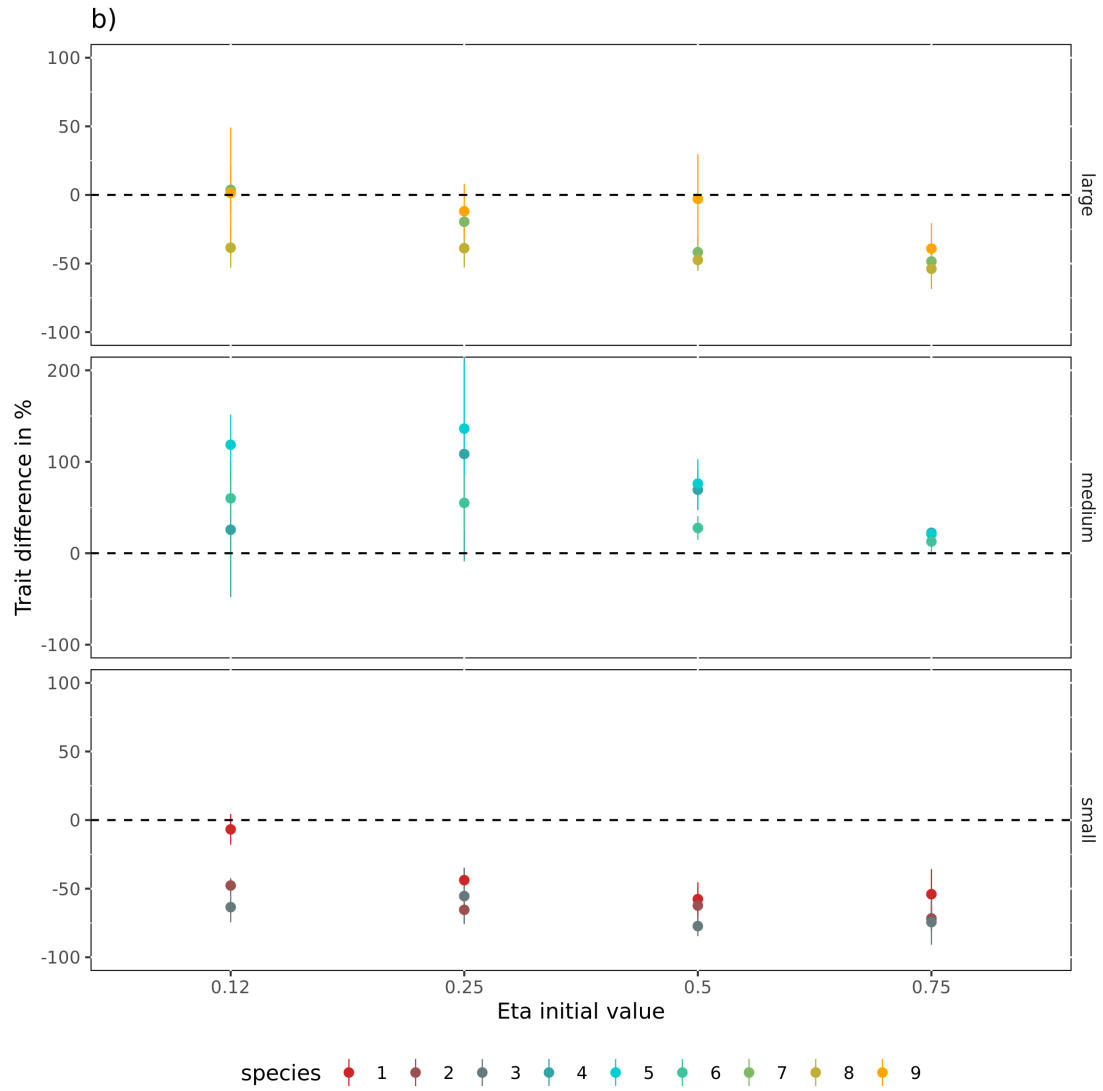
The robustness of our model outcomes to parameter assumptions was explored in an extensive set of simulations. In these sensitivity analyses we are mostly looking at the qualitative difference in results, i.e. whether the direction of evolutionary change in maturation size (up or down from the initial value) is the same as in the baseline scenarios. We are less concerned about the absolute quantitative change. Changing the initial η (Fig.S.1) resulted in different final η values for some of the medium-sized species and, to a lesser extent, the large species, but the range of values we explored led to qualitatively similar trait changes by the end of the simulation and did not affect our overall conclusions. Regardless of the initial values of η , by the end of the 3000 years, they all declined in small bodied species, and mostly increased in the middle sized species.

We assessed whether our assumptions about key predation parameters – predator-prey mass ratio (β) and width of predation kernel (σ) - affected the direction (increase or decrease) in maturation size change at the end of 6000-year simulation period. We found that, although the magnitude of the change varied somewhat, for all species the direction of evolutionary trends were generally the same as in the baseline scenario. The only exception was for the highly variable species 4 and especially 5, when β or σ values were very small (50 and 0.9 respectively) (Figs.S.6,S.5).

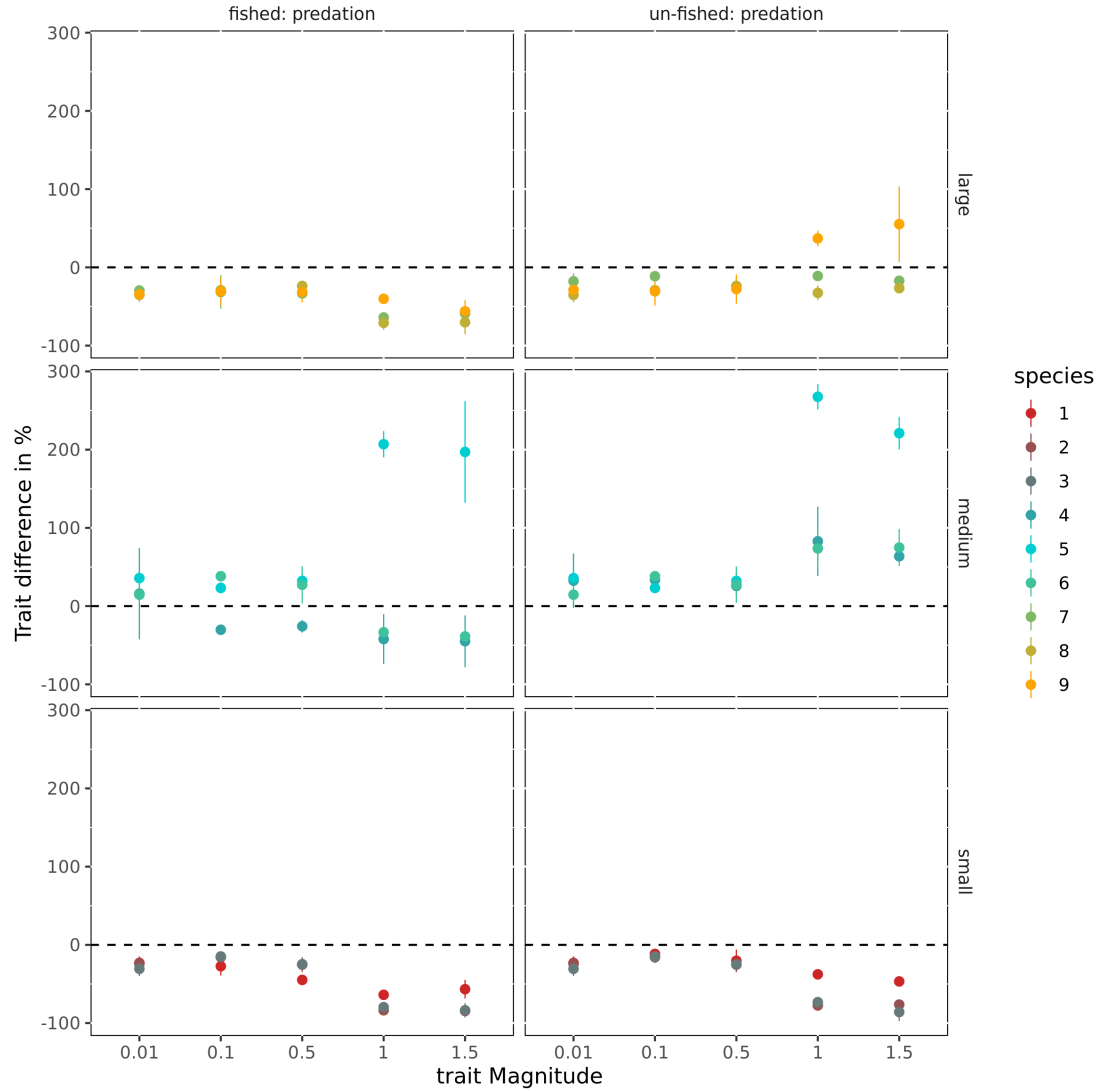
Next, we explored sensitivity of model output to four parameters determining the rate of evolution: the magnitude of trait change, the phenotype appearance rate (χ) and the phenotype abundance upon introduction. The rate at which new

886 phenotypes were introduced (χ) affected the speed of evolution, and almost no
887 evolution occurred when the rate was 10 to 100 times slower than in the main
888 simulation set (Fig.S.3). Yet, a 50% increase in χ gave qualitatively similar re-
889 sponses to fishing. Similarly, the magnitude of change between new and parent
890 phenotypes determined the rate of evolution, where large amplitude of changes
891 led to faster evolution, yet the qualitative response to fishing remained the same
892 (Fig.S.2). Similarly, changing the initial abundance of a new phenotype along
893 a continuum from 0.01% to 10% of the parent's abundance led to very similar
894 evolutionary responses to those reported in the main text.

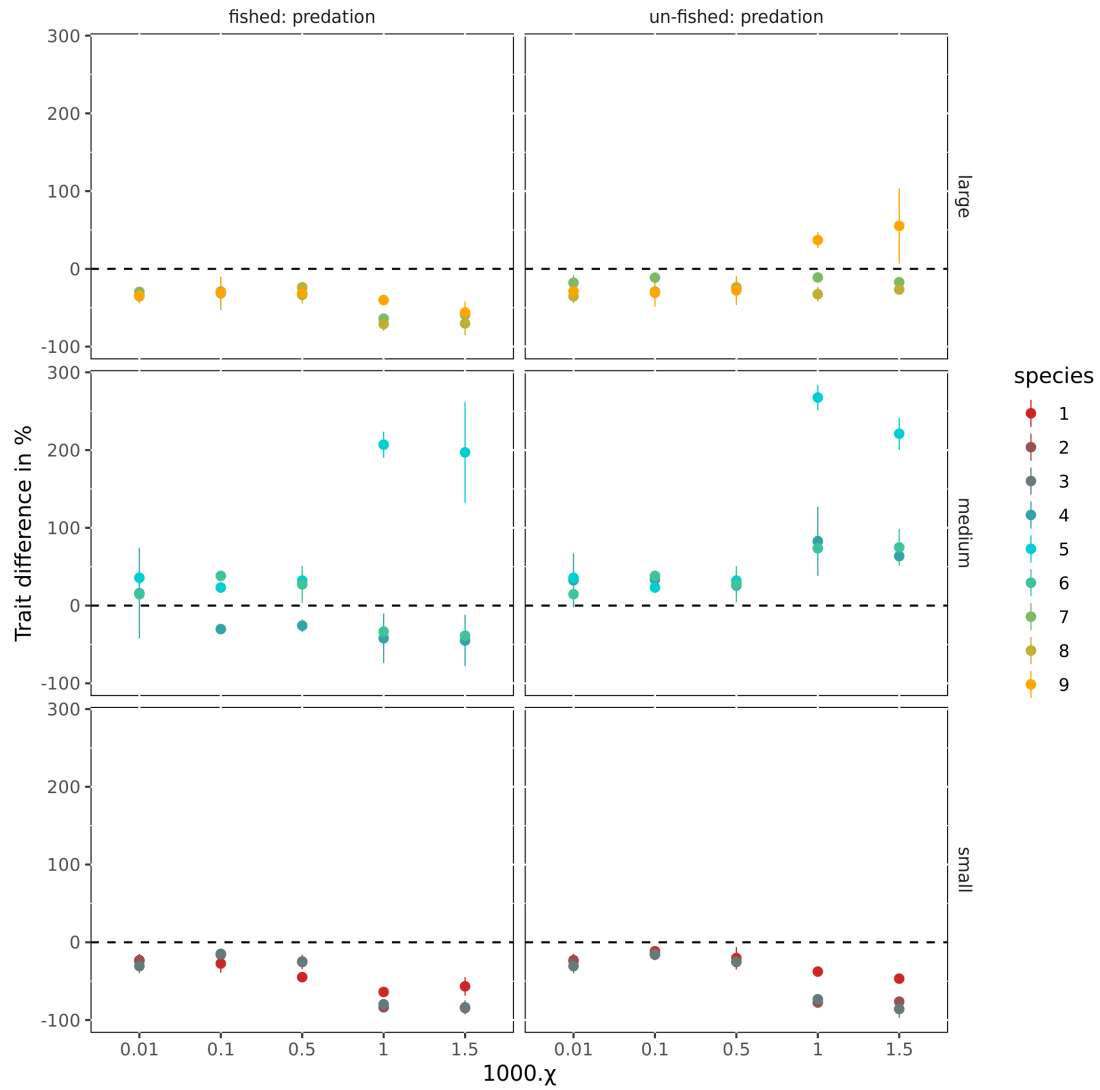
895 Finally, increasing the number of replications per scenario from 10 to 50 (in
896 the scenario with predation and fishing) did not strongly affect the observed vari-
897 ation and demonstrated that 10 replications were largely sufficient to capture the
898 variation and trends in trait evolution; the size of standard deviation bars remains
899 the same across different replication values (Figs.S.7,S.8).



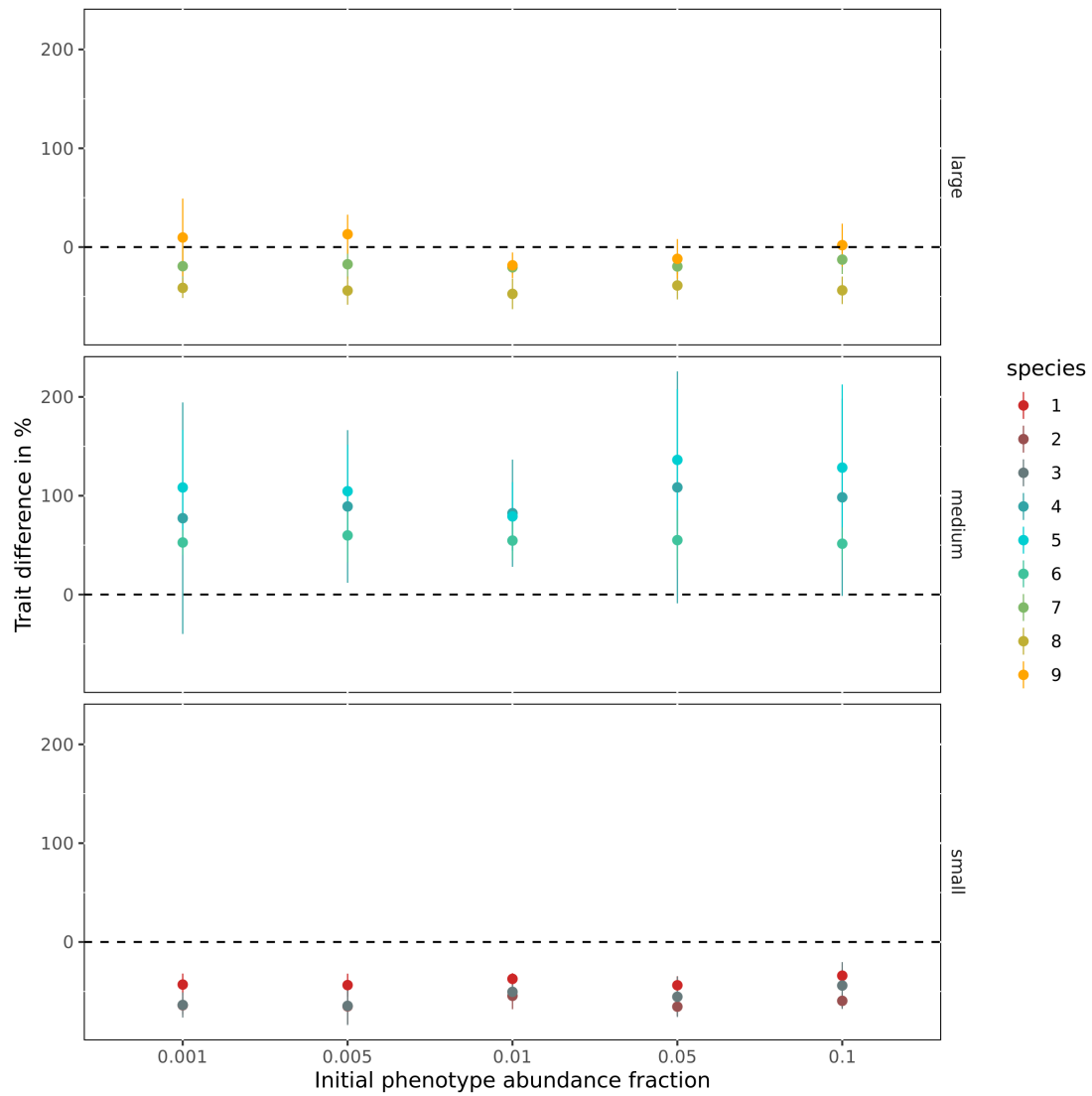
Supplementary Figure S.1: Effect of varying the initial η value on the evolution of trait value at the end of 3000 year simulation before fishing is started. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 0.25. Sensitivity analysis shows that the overall direction of trait change (up or down from the dashed line) remains similar across the range of initial η values



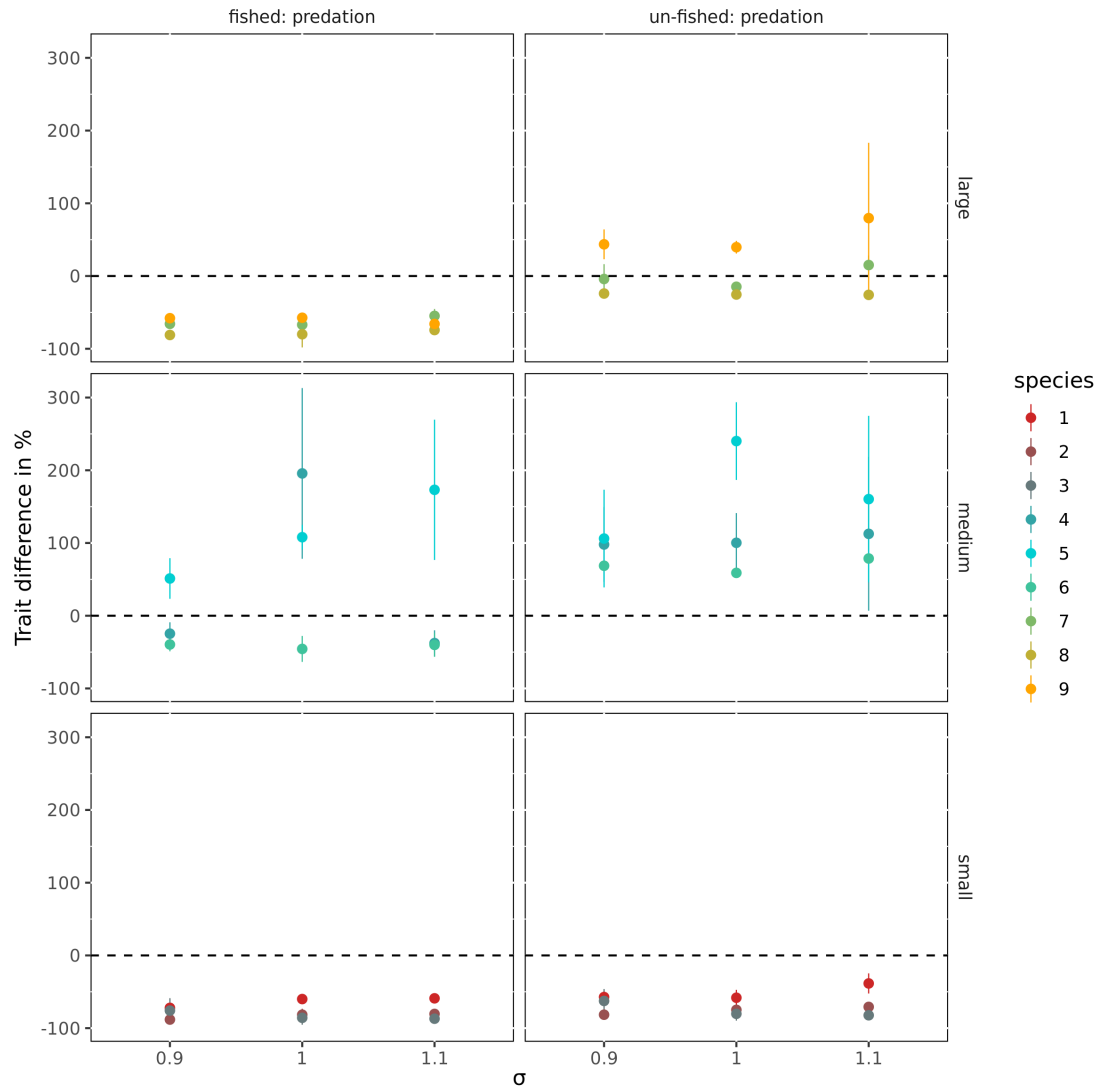
Supplementary Figure S.2: Effect of varying the magnitude of the trait evolution after 6000 years. The trait magnitude determines the maximum percentage difference possible between parent and new trait's phenotype. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 0.2.



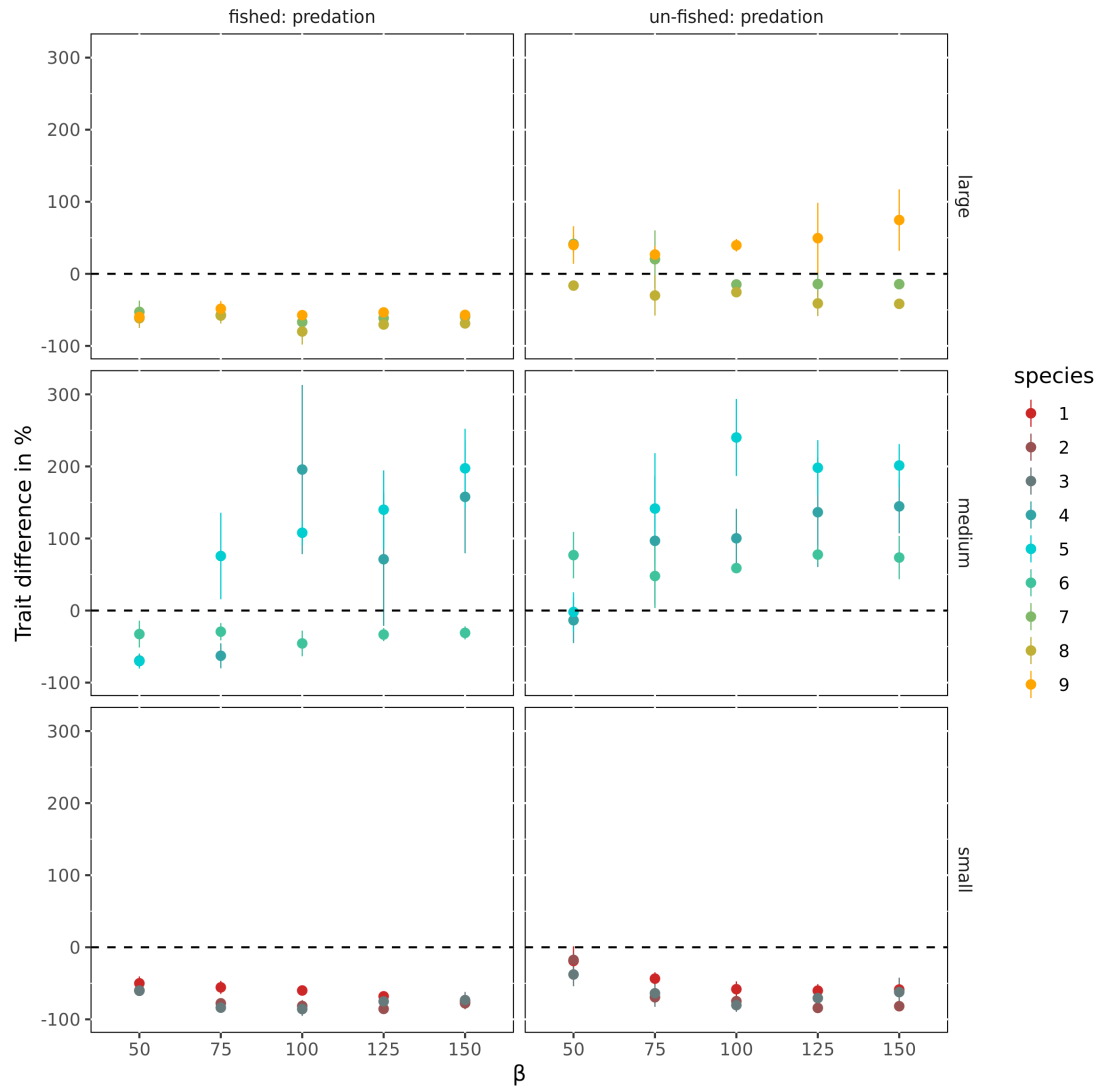
Supplementary Figure S.3: Effect of varying the χ parameter on the trait evolution after 6000 years. The χ parameter determines the probability of new phenotype appearance. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 0.001.



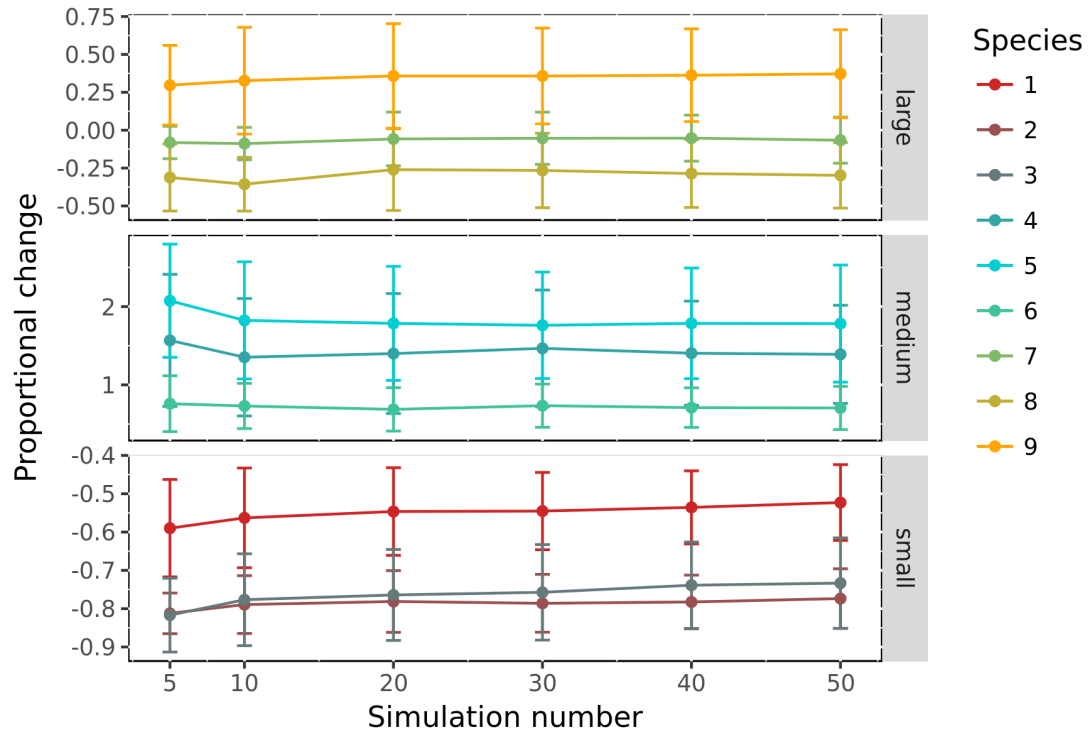
Supplementary Figure S.4: Effect of varying the initial phenotype abundance upon introduction at the end of 3000 year simulation before fishing is started. This parameter determines what fraction of a parent's biomass is used as an initial biomass for new phenotypes. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 0.05.



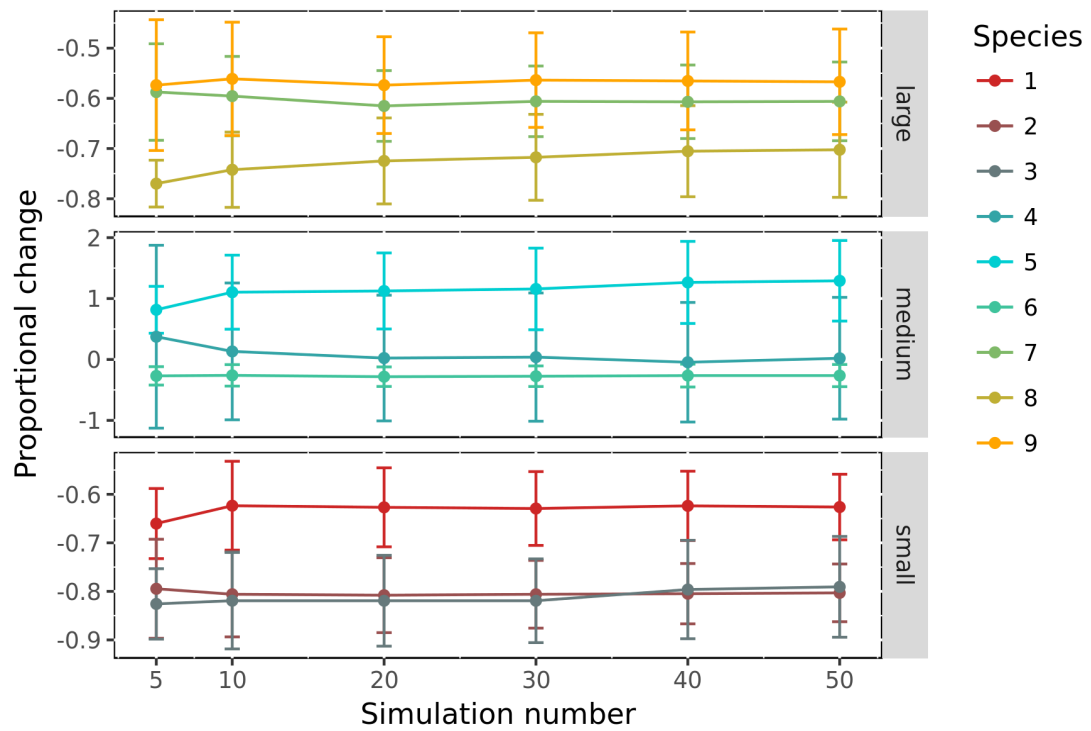
Supplementary Figure S.5: Effect of varying the σ parameter on the trait evolution after 6000 years. The σ parameter determines the width of the feeding kernel. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 1.



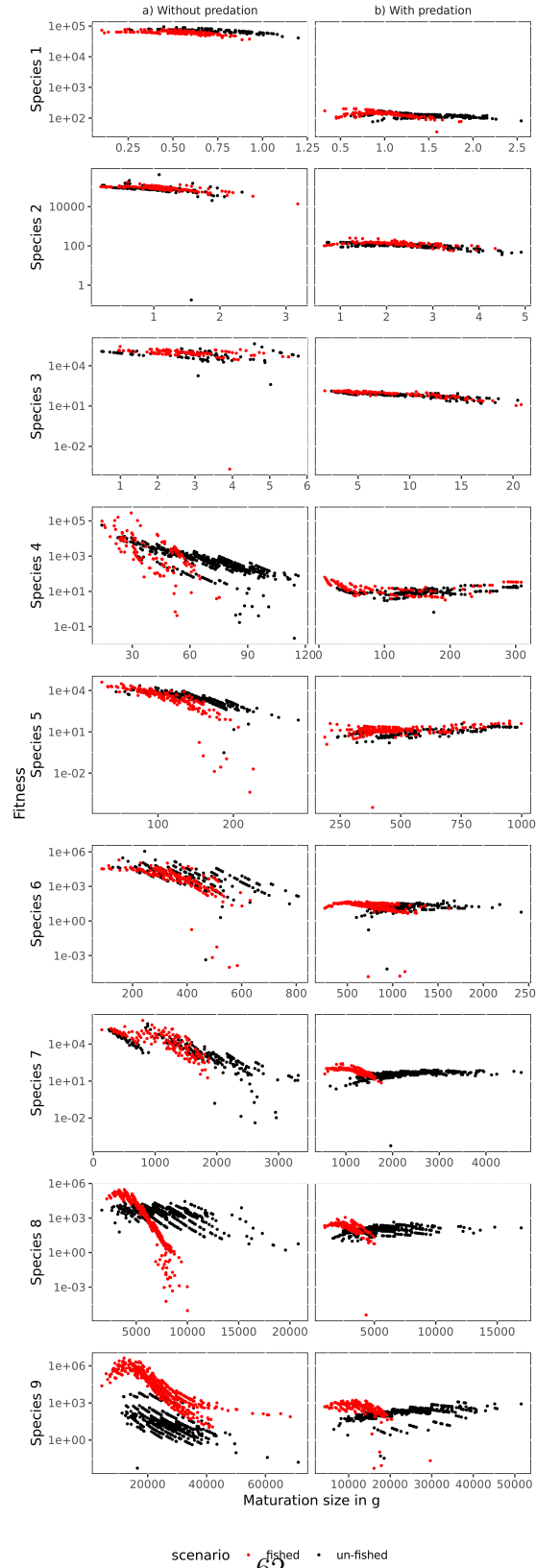
Supplementary Figure S.6: Effect of varying the β parameter on the trait evolution after 6000 years. The β parameter determines the preferred predator-prey mass ratio. Values show the % difference in trait value between start and end of the simulation. Error bars show the standard deviation for each set of parameter values tested. The parameter value used in the main simulation is 100.



Supplementary Figure S.7: Effect of increasing number of simulations on the patterns of trait evolution in simulations without fishing (year 6000). The trait's value per species are plotted against the number of simulations to determine the minimum number of runs necessary to have robust results. Error bars show the standard deviation of the results, demonstrating that variation across simulations is captured sufficiently well with 10 replications used in the main analyses.



Supplementary Figure S.8: Effect of increasing number of simulations on the patterns of trait evolution in simulations with fishing (year 6000). For other details see legend of Fig.S.7.



Supplementary Figure S.9: Species' fitness across simulations. Each dot shows fitness of a phenotype with different maturation size in scenarios with (red) and without (black) fishing across simulations. The figure shows phenotypes in a cohort starting at year 5500 in simulations without (a) and with (b) predation.

Supplementary Table S.1: Model selection table. df is degrees of freedom; logLik is likelihood; AICc is Akaike information criterion; delta is change in AICc. fsh - fishing, prd - predation, sp - species (all treated as factors). The best model is on the top row and includes all factors and their interactions. The second best model (second row) does not include the three-way interaction.

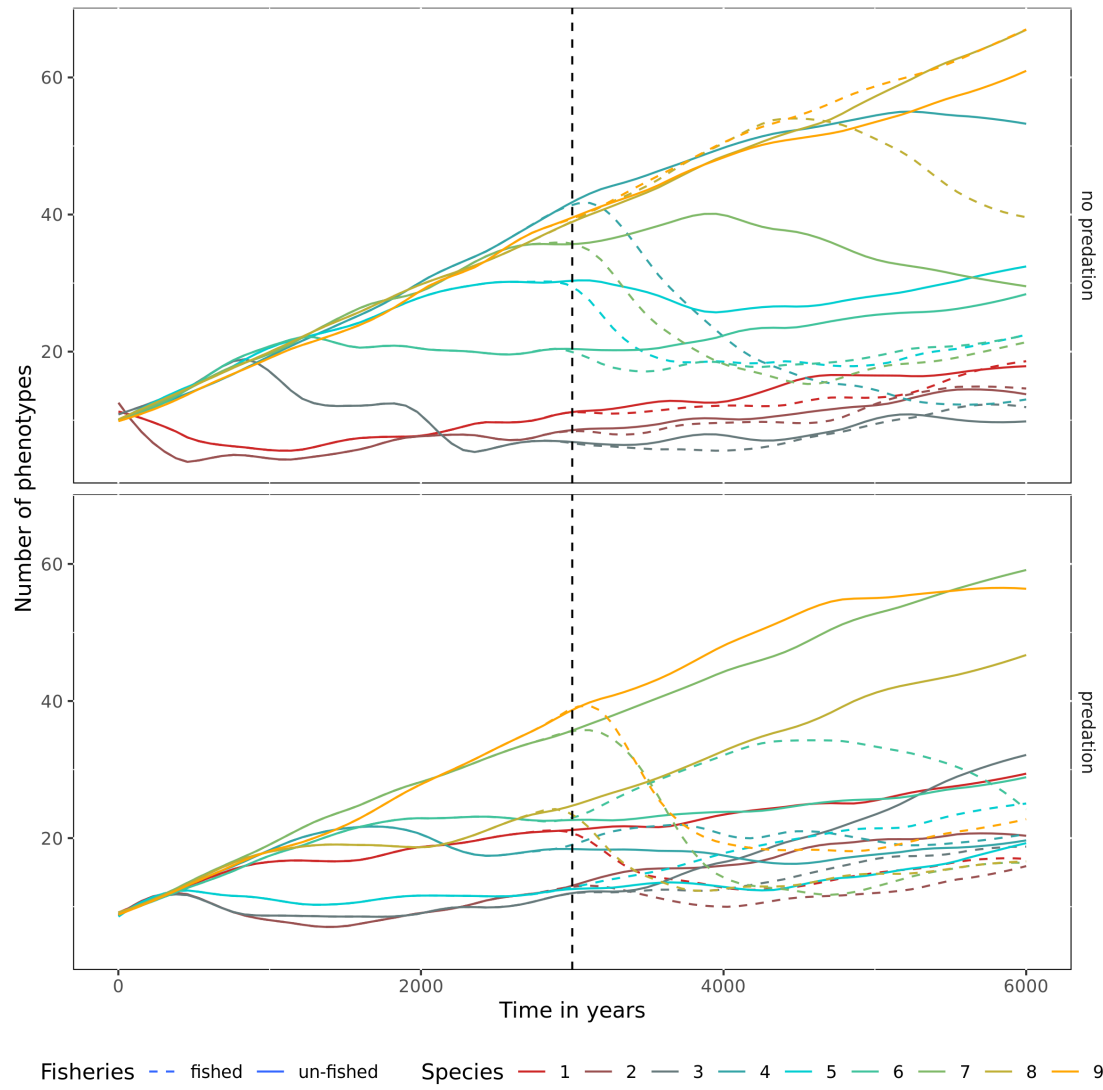
	(Intercept)	fsh	prd	sp	fsh:prd	fsh:sp	prd:sp	f:p:s	df	logLik	AICc	delta
128	-3.2	+	+	+	+	+	+	+	37	-147.38	377.49	0
64	-3.12	+	+	+	+	+	+		29	-158.61	380.5	3.01
56	-3.19	+	+	+		+	+		28	-164.83	390.57	13.08
48	-3.29	+	+	+	+		+		21	-190.11	424.96	47.47
40	-3.36	+	+	+			+		20	-195.35	433.18	55.69
39	-3.13		+	+			+		19	-241.79	523.82	146.33
32	-3.02	+	+	+	+	+			21	-274.09	592.91	215.42
24	-3.09	+	+	+		+			20	-277.39	597.26	219.77
16	-3.19	+	+	+	+				13	-291.36	609.77	232.28
8	-3.26	+	+	+					12	-294.36	613.62	236.13

Supplementary Table S.2: ANOVA table for the 3-way model $\log(\eta)$ Species*Predation*Fishing. Partial effects sizes for each term are also reported (pes). Model is the first line of table [S.1](#)

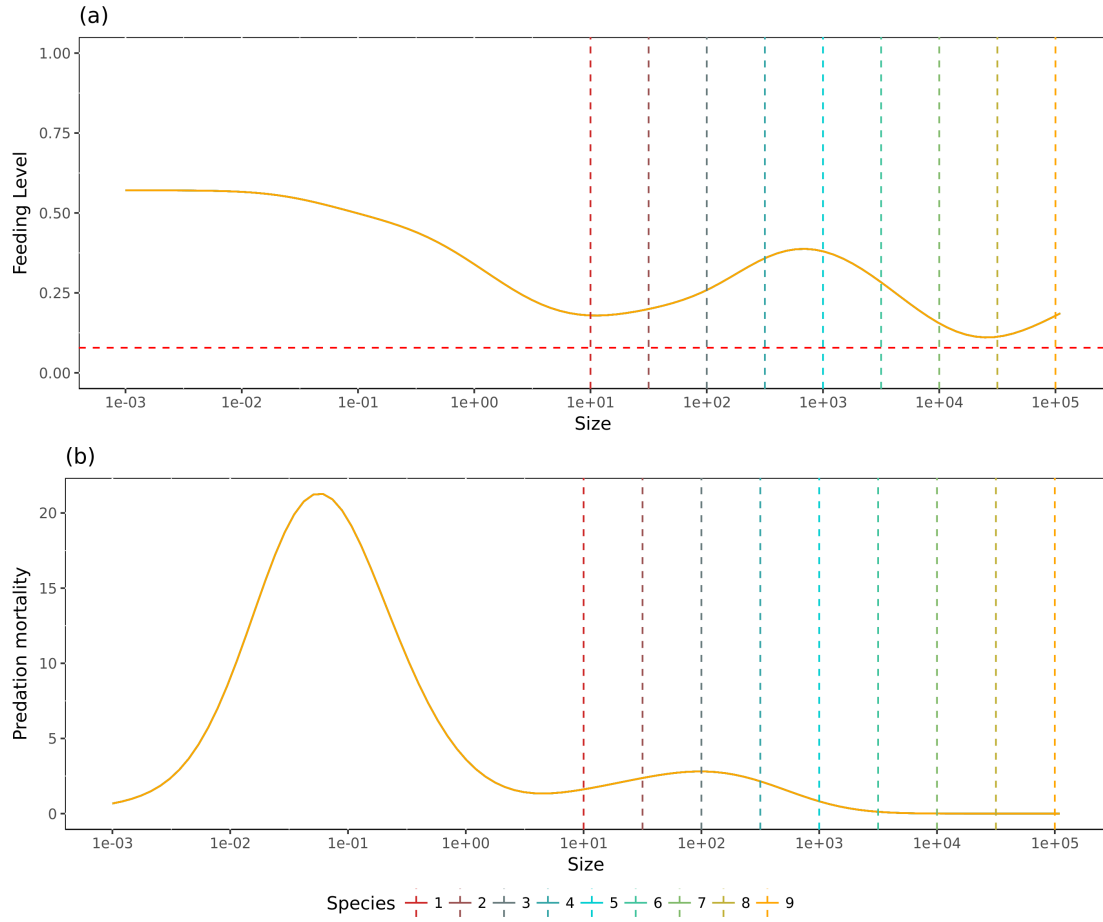
	Df	Sum Sq	Mean Sq	F value	Pr(>F)	pes
species	8	190.27	23.78	161.22	0	0.79
predation	1	42.14	42.14	285.65	0	0.46
fisheries	1	18.36	18.36	124.5	0	0.27
species:predation	8	45.75	5.72	38.77	0	0.48
species:fisheries	8	9.73	1.21	8.24	0	0.16
predation:fisheries	1	1.78	1.78	12.12	0	0.03
species:predation:fisheries	8	3.07	0.38	2.6	0.01	0.06
Residuals	324	47.79	0.14	NA	NA	NA

Supplementary Table S.3: Empirical size data and their references used in Fig.6

Species	Maturation size	Asymptotic size	References
Cod	3337.375666	19428.63866	Jennings et al. 1998
Haddock	334.656743	3117.98674	Jennings et al. 1998
Herring	111.102066	221.41796	Goodwin et al. 2006
Norway pout	46.924711	86.11638	Jennings et al. 1998
Plaice	203.236035	1496.00467	Jennings et al. 1998
Saithe	1459.741393	45627.15377	Jennings et al. 1998
Sandeel	3.563648	34.52603	Goodwin et al. 2006
Sole	150.154812	684.44291	Jennings et al. 1998
Sprat	15.674781	32.24996	Bailey 1980
Whiting	60.689	612.10952	Jennings et al. 1998
Dab	21.712738	211.24228	Rijnsdorp et al. 1992
Grey Gurnard	103.313363	886.01239	Fishbase
Anoplopoma fimbria	2243.365824	3388.987552	Olsson and Gislason, 2016
Anoplopoma fimbria	2495.410527	2591.429307	Olsson and Gislason, 2016
Sebastes crameri	839.2709096	1623.941784	Olsson and Gislason, 2016
Sebastes elongatus	114.0872975	727.4969882	Olsson and Gislason, 2016
Sebastes flavidus	1159.479145	2013.986983	Olsson and Gislason, 2016
Clupea harengus	144.4055108	234.7223797	Olsson and Gislason, 2016
Clupea harengus	152.5260593	306.5630249	Olsson and Gislason, 2016
Clupea harengus	127.5720137	219.7998486	Olsson and Gislason, 2016
Clupea harengus	215.6687028	367.248827	Olsson and Gislason, 2016
Clupea harengus	122.5440299	245.7383233	Olsson and Gislason, 2016
Clupea harengus	236.954886	382.5939548	Olsson and Gislason, 2016
Clupea harengus	240.5513444	330.4041016	Olsson and Gislason, 2016
Clupea pallasii	120.1927067	215.8984944	Olsson and Gislason, 2016
Clupea pallasii	173.2437888	453.506854	Olsson and Gislason, 2016
Clupea pallasii	66.6359996	215.8984944	Olsson and Gislason, 2016
Gadus macrocephalus	1448.78265	11769.19016	Olsson and Gislason, 2016
Gadus morhua	5825.230626	22718.35315	Olsson and Gislason, 2016
Gadus morhua	3472.860386	20086.52614	Olsson and Gislason, 2016
Gadus morhua	2288.576711	10111.50945	Olsson and Gislason, 2016
Gadus morhua	2021.927647	3262.315803	Olsson and Gislason, 2016
Gadus morhua	1190.137173	1645.589879	Olsson and Gislason, 2016
Gadus morhua	1768.349977	14147.75821	Olsson and Gislason, 2016
Melanogrammus aeglefinus	293.170736	3279.323679	Olsson and Gislason, 2016
Melanogrammus aeglefinus	698.1900651	2630.904545	Olsson and Gislason, 2016
Melanogrammus aeglefinus	707.9575712	3834.294493	Olsson and Gislason, 2016
Merlangius merlangus	179.256487	1495.422983	Olsson and Gislason, 2016
Merlangius merlangus	62.34150354	620.9007471	Olsson and Gislason, 2016
Theragra chalcogramma	294.78	3014.60454	Olsson and Gislason, 2016
Theragra chalcogramma	379.8975	730.02	Olsson and Gislason, 2016
Theragra chalcogramma	555.66	1509.22542	Olsson and Gislason, 2016
Trisopterus esmarkii	42.4700496	76.1849616	Olsson and Gislason, 2016
Hippoglossoides platessoides	878.5564359	5363.615599	Olsson and Gislason, 2016
Pleuronectes ferruginae	231.7439325	623.8158895	Olsson and Gislason, 2016
Pleuronectes ferruginae	141.712941	706.969943	Olsson and Gislason, 2016
Pleuronectes platessa	251.4994817	2287.908563	Olsson and Gislason, 2016
Pleuronectes platessa	188.4555558	1049.062573	Olsson and Gislason, 2016
Pleuronectes platessa	197.3690262	1749.712324	Olsson and Gislason, 2016
Solea solea	134.6253253	1233.978732	Olsson and Gislason, 2016
Solea solea	145.1377053	591.8365986	Olsson and Gislason, 2016
Carcharhinus brevipinna	57578.96575	178213.8916	Olsson and Gislason, 2016
Carcharhinus falciformis	79173.44259	181720.6787	Olsson and Gislason, 2016
Carcharhinus isodon	8814.472849	18111.37362	Olsson and Gislason, 2016
Carcharhinus limbatus	15063.79472	26326.34765	Olsson and Gislason, 2016
Carcharhinus sorrah	8153.456825	22868.00295	Olsson and Gislason, 2016
Carcharhinus sorrah	4704.774274	11108.36879	Olsson and Gislason, 2016
Carcharhinus tilstoni	11054.41718	48226.29158	Olsson and Gislason, 2016
Galeorhinus galeus	13556.40429	23279.53846	Olsson and Gislason, 2016
Mustelus antarcticus	5515.412778	37633.86675	Olsson and Gislason, 2016
Mustelus antarcticus	5840.80978	48712.8062	Olsson and Gislason, 2016
Prionace glauca	203867.6355	371380.9422	Olsson and Gislason, 2016
Menidia menidia	2.3	9.3	Conover and Munch, 2002
Menidia menidia	3.8	10	Conover and Munch, 2002
Menidia menidia	5.2	10.5	Conover and Munch, 2002
Poecilia reticulata	0.0761	0.590746429	Reznik et al., 1997
Poecilia reticulata	0.0675	0.590746429	Reznik et al., 1997
Poecilia reticulata	0.1892	3.602635961	Reznik et al., 1997
Poecilia reticulata	0.1623	3.602635961	Reznik et al., 1997
Danio rerio	0.0749	0.2134	Ulloa et al., 2011



Supplementary Figure S.10: Number of phenotypes through time per species averaged across all stochastic realisations. The vertical line shows the introduction of fisheries and the dashed line shows phenotype numbers in simulations with fishing.



Supplementary Figure S.11: Feeding level and predation mortality through sizes for one un-fished stochastic simulation after 6000 years of evolution. Parameters that determine feeding and predation are the same between species so their profiles overlap. The vertical dashed lines show the asymptotic size of each species. a) shows the feeding level, where 1 is the maximum feeding level defined by the maximum intake rate. The horizontal red line indicate the critical feeding level, below which starvation mortality applies. b) shows the instantaneous predation mortality value.