

Age is not just a number – senescence affects how fish populations respond to different fishing regimes

Pauliina Anna Ahti (✉ pauliina.a.s.ahti@jyu.fi)

University of Jyväskylä <https://orcid.org/0000-0002-6216-9616>

Silva Uusi-Heikkilä

University of Jyväskylä: Jyväskylän Yliopisto

Timo J Marjomäki

University of Jyväskylä: Jyväskylän Yliopisto

Anna Kuparinen

University of Jyväskylä: Jyväskylän Yliopisto

Original Research

Keywords: senescence, life-history, trade-offs, eco-evolutionary dynamics, body size, fisheries, selection

Posted Date: February 16th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-184938/v1>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

1

2 **Age is not just a number – senescence affects how fish populations**

3 **respond to different fishing regimes**

4 **Pauliina A. Ahti^{1,2*}, Silva Uusi-Heikkilä¹, Timo J. Marjomäki¹, Anna Kuparinen¹**

5 ¹ Department of Biological and Environmental Sciences, P.O. Box 35, 40014 University
6 of Jyväskylä, Finland

7 ² Institute of Biodiversity, Animal Health, and Comparative Medicine, College of Medical,
8 Veterinary, and Life Sciences, University of Glasgow, Glasgow, G12 8QQ UK

9 * Corresponding author: Pauliina A. Ahti, Department of Biological and Environmental
10 Sciences, P.O. Box 35, 40014 University of Jyväskylä, Finland, telephone: +358-41-
11 492-4459, e-mail: pauliina.a.s.ahti@jyu.fi

12 **Running title:** Senescence improves fish population resiliency

13 **Keywords:** senescence, life-history, trade-offs, eco-evolutionary dynamics, body size,
14 fisheries, selection

15 **Total word count:** 6800

16 **Number of figures:** 4

17 **Number of tables:** 1

18 Appendix 1, Appendix 2, Appendix 3

19

20

21 **Abstract**

22 The presence of senescence in natural populations remains an unsolved problem in
23 biology. Described as an age-dependent increase in natural mortality (known as
24 actuarial senescence) and an age-dependent decrease in fecundity (known as
25 reproductive senescence), the role of senescence in nature is still poorly understood.
26 Based on empirical estimates of reproductive and actuarial senescence, we explored
27 how senescence affects the population dynamics of *Coregonus albula*, a small,
28 schooling salmonid fish. Using an empirically-based eco-evolutionary model, we
29 investigated how the presence or absence of senescence affects how the fish
30 population responds to pristine, intensive harvest, and recovery phases. Our results
31 showed that at an individual level, the presence of senescence was accompanied by
32 life-history trade-offs, i.e. lower asymptotic length and smaller size and younger age at
33 maturity, both in the presence and absence of fishing. At the population level, the
34 response to different fisheries selection patterns depended on the presence or absence
35 of senescence. Importantly, the results indicate that through the lifehistory trade-offs
36 between early reproduction and late life survival, the young and small individuals can
37 have an important role in population recovery, especially when senescence is present.
38 Since most life-history and fisheries models ignore senescence, they may be over-
39 estimating reproductive capacity and under-estimating natural mortality. Our results
40 highlight the need for increasing biological realism in these models to ensure the
41 successful management of our natural resources.

42

43

44 **Introduction**

45 Senescence is considered a fundamentally fitness decreasing trait, and its presence
46 and role in natural populations remains an unsolved problem in biology (Monaghan et
47 al. 2008; Selman et al. 2012; Nussey et al. 2013). Senescence is described as age-
48 dependent increase in natural mortality (known as actuarial senescence), and age-
49 dependent decrease in fecundity (known as reproductive senescence). For much of the
50 20th century it was thought that very few animals in the wild experience senescence
51 because external factors such as predators, diseases or environmental stressors would
52 kill them before the consequences of aging would commence (Medawar 1952). Today,
53 it is well known that this is not the case and evidence for senescence across taxa is
54 accumulating (Nussey et al. 2013). Several studies of wild populations have shown that
55 trade-offs exist between early and late life performance (Jensen 1996; Bonsall and
56 Mangel 2004; Lemaitre et al. 2014; Maklakov and Chapman 2019), likely contributing to
57 the onset or development of senescence in an individual. The early vs. late life
58 performance has been tested in many vertebrates and has gained a lot of support, but
59 tests in fishes are scarce, mainly owing to the difficulty of testing for senescence in
60 species with indeterminate growth (Heino and Kaitala 1999; Reznick et al. 2002;
61 Lemaître et al. 2015).

62 Life-history trade-offs may take place between functions as well as within the same
63 function. For instance, increased growth rate and increased reproductive effort early in
64 life and higher natural mortality rate later in life are known to be linked (Kirkwood and
65 Rose 1991; Lester et al. 2004). Similarly, investment in future reproductive effort is
66 thought to be of lesser value in terms of fitness benefits than current reproductive effort,

67 mainly due to the uncertainty of future reproduction (Zhang and Hood 2016). Following
68 the close link between life history characters and senescence, it is therefore likely, as
69 hypothesised by Benoît *et al.* (2018), that assuming that increased allocation to
70 reproduction in early life leads to an increased rate of ageing later, fishing-induced
71 changes in maturation age and senescence could actually be linked. Indeed, the natural
72 mortality rate of many fish populations is thought to have increased in the recent
73 decades (Gislason *et al.* 2010).

74 While most fishes express indeterminate growth and high longevity (Carey and Judge,
75 2000), it has been suggested that fish experience delayed senescence relative to birds
76 and mammals, facilitated in part by the capacity for increasing fecundity with age
77 (Reznick *et al.* 2002). Indeed, female body size and reproductive output in fish are
78 known to be positively correlated, indicating that the older and larger the fish, the higher
79 its reproductive output. Most fisheries and fish population models (Beverton-Holt, 1957;
80 Enberg *et al.*, 2010; Andersen and Beyer, 2015; Zimmermann and Jørgensen, 2015)
81 and life-history models (Roff, 1983; Brunel *et al.*, 2013; Charnov *et al.*, 2013) assume
82 that body size (weight) scales isometrically with reproductive output. Recent meta-
83 analysis has provided cues that the scaling might even be hyper-allometric in some
84 cases (Barneche *et al.* 2018), further stressing the role of large and old individuals for
85 population growth or, in case of over-exploitation, for recovery. Additionally, in fisheries
86 and life-history models, the natural mortality of fish is often assumed to be independent
87 of the age or size of the fish (Gislason *et al.* 2010). Models with increasing fecundity
88 with age and size, and age- and size-independent natural mortality essentially describe
89 fish as having no reproductive or actuarial senescence at all.

90 While rarely included in fisheries and life-history models, senescence in fish was first
91 documented over 60 years ago (Gerking 1957; Comfort 1960, 1963; Woodhead and
92 Ellett 1966, 1967, 1969a, b). Over the past few decades, evidence for both reproductive
93 (Reznick et al. 2006; Benoît et al. 2018) and actuarial (Beverton et al. 2004; Uriarte et
94 al. 2016) senescence as well as general deterioration with age (Patnaik et al. 1994;
95 Hendry et al. 2004; Morbey et al. 2005; Carlson et al. 2007) in fish has started to
96 accumulate. While the importance of old and large individuals for the reproductive pool
97 is evident, the common conservation measure of relying on the reproductive effort of
98 large individuals could have detrimental effects on the recovery and resilience of fish
99 populations if actuarial or reproductive senescence is indeed wide-spread in fishes (Le
100 Bris et al. 2015). Given that senescence influences the reproductive outcome and
101 natural mortality rate, it would also have major consequences to our understanding of
102 fish population dynamics and would thereby affect our management efforts of fish
103 populations.

104 Sustainable fish populations are vital not only for food security around the world (Merino
105 et al. 2012), but also for healthy biodiversity and climate regulation (Jackson 2008).
106 Several fish populations that have collapsed as a result of fishing, have not recovered or
107 are recovering slower than expected even after significant declines in fishing effort
108 (Hutchings and Reynolds 2004). The reasons behind the lack of recovery are complex
109 and likely include factors such as habitat destruction, climatic conditions, trends in prey-
110 predator relationships, and changes in life-history traits (Dulvy et al. 2003a; Hutchings
111 and Reynolds 2004; Olsen et al. 2009). While much research effort has been put into
112 understanding the links between life-history traits such as body size, growth rate, size

113 and age at maturity, and population dynamics (Ahti et al. 2020), the role of reproductive
114 and actuarial senescence in population dynamics and population recovery remains
115 poorly understood.

116 Monitoring and measuring reproductive or actuarial senescence in nature is notoriously
117 difficult, particularly for fish, and the fishes with the most data tend to be the fishes that
118 are the most heavily fished, therefore likely caught before senescence commences.

119 Here, we used empirical data to parameterise an existing eco-evolutionary model
120 (Kuparinen et al. 2011) to overcome these obstacles and to illuminate the role of
121 senescence in fish population dynamics and population recovery under two different
122 fishery selection schemes. As opposed to experimental or empirical studies, the
123 simulation model allows us to control the presence and absence of senescence and
124 explore how, all else being equal, it influences fish population dynamics in the presence
125 and absence of fishing. We used vendace (*Coregonus albula*, Linnaeus), an
126 economically and culturally important freshwater salmonid, as a model species.

127 Specifically, we address the following questions: 1) How does the presence or absence
128 of senescence influence the population dynamics of fish, in terms of biomass and
129 number of fish prior to fishing? And 2) how does the response to different fishery
130 selection schemes differ depending on the presence or absence of senescence? Our
131 results provide insights into the effects of senescence on population dynamics before,
132 during, and after harvest, and how including it in fisheries and life-history models may
133 improve our understanding of population dynamics and facilitate management efforts.

134 **Materials and methods**

135 To explore the role of senescence in *Coregonus Albula* (Linnaeus) life-histories and
136 populations, we used an individual-based model that incorporates empirical growth,
137 fecundity, and survival data with the principles of quantitative genetics and demographic
138 processes. The core of this mechanistic model lies in the strong negative correlations
139 among the von Bertalanffy (vB) growth model parameters L_∞ (asymptotic length), and k
140 (intrinsic growth coefficient, i.e. how fast the fish length is approaching L_∞) and the size
141 at maturity (von Bertalanffy 1938, 1949; Quince et al. 2008). Since the simulation model
142 has been described in detail elsewhere (Kuparinen et al. 2011), we will here limit the
143 model description to a general description of the modelling approach and the main
144 features and additions specific to our study design. While the empirical data are from
145 Lake Puulavesi in Central Finland, the results can be generalised to any fish with similar
146 life-history properties.

147 *General description of the modelling approach*

148 The eco-evolutionary model includes five main components (Fig 1a - e). These are four
149 dependent sets of variables: growth, fecundity, survival, population demographics, and
150 an independent variable: senescence.

151 Life history traits such as size and age at maturity are thought to be controlled by many
152 loci (Roff 2002). In fishes, the correlation of size at maturity and L_∞ is a well-known life-
153 history invariant (Charnov 1993). Thus, in the growth component (Fig. 1a), we utilised
154 empirical length-at-age data back-calculated from fish scales to model the L_∞ . The L_∞
155 was set to be an evolving trait so that the genotype coding L_∞ of each individual was
156 described by 10 diploid loci with two alleles in each. The alleles were inherited in the
157 classic Mendelian way, so that each offspring received one randomly drawn allele from

158 the mother, and one from the father. Each allele was coded as 0 or 1 and the sum of
159 alleles across the ten loci was coupled with a normally distributed random number
160 (mean zero) to describe phenotypic variability, and then the sum was linearly translated
161 to values of L_{∞} . The standard deviation of the normally distributed random number was
162 adjusted to yield a realistic heritability of 0.2-0.3 (Mousseau and Roff 1987). The vB
163 growth parameter k and the size at maturity were then determined based on L_{∞} . (For
164 more on k see below “Model parametrisation”). We used the empirical data to determine
165 that the maturation size threshold was at 67% of their L_{∞} (mean size at 2 years of age)
166 and no earlier than on their second autumn, which is in line with literature (Jensen
167 1998; Karjalainen et al. 2016). This way, we ensured that the fish in the model will
168 mature once they reach 67% of their L_{∞} , but never before they reach their second
169 autumn. Thus, fish younger than two years old, or two-year-olds smaller than 67% of
170 their L_{∞} could not yet reproduce.

171 The fecundity component (Fig. 1b) is based on a length-weight relationship, which was
172 specifically calculated for *C. albula* from Lake Puulavesi. Using this length-weight
173 relationship and published empirical data on egg numbers and female weights
174 (Karjalainen et al. 2016), we fitted a linear model for the fecundity-weight relationship.
175 The survival component (Fig. 1c) includes an empirically based (Marjomäki et al. 2014;
176 Karjalainen et al. 2016) probability ($P = 0.002$) for a fertilized egg to hatch and the
177 juvenile to survive until 2 years of age. The sex of the juveniles was drawn from a
178 Bernoulli trial with a probability of 0.5. Mating occurred randomly, so that for each
179 mature female a random mate was drawn from a group of mature males. The maximum

180 lifetime for each individual was limited to 6 years, according to local estimations in Lake
181 Puulavesi (Marjomäki and Huolila 1994).

182 The population component (Fig. 1d) describes density dependency so that at 75% of
183 the population carrying capacity, the individual growth is reduced to 50% of that
184 predicted by the individual's vB growth curve (its L_∞ and k parameters). Additionally, egg
185 production was set to be density dependent so that the closer the population was to its
186 carrying capacity, the fewer eggs were produced.

187 The fifth component of the eco-evolutionary model describes senescence in its two
188 forms: reproductive senescence and actuarial senescence (Fig. 1e). The reproductive
189 senescence was modelled by multiplying the linear model for fecundity by the
190 gonadosomatic index (GSI) for the year class in question. When no reproductive
191 senescence was modelled, only the linear model for fecundity was used. Actuarial
192 senescence was modelled by increasing the rate of natural mortality each year, as
193 opposed to keeping natural mortality rate constant throughout lifetime as in the scenario
194 with no actuarial senescence. All the other components were kept identical in the
195 simulations (Fig. 1f), but the presence and absence of reproductive and actuarial
196 senescence was altered.

197 Each population in each scenario was then allowed to "live" for 500 years, and the
198 individuals and populations were traced at annual time steps. At each annual step, the
199 growth, reproduction, and mortality of each individual fish was simulated to get the
200 population data for the next year. During those 500 years, the populations experienced
201 three consecutive phases: 200 years of pristine phase, 100 years of intense fishing, and
202 200 years of recovery (Fig. 1f). The output data of particular interest, i.e. asymptotic

203 length (L_∞), biomass (BM), and number of fish (N) was collected annually. Each
204 simulation was replicated 100 times.

205 *Parametrisation of the model*

206 The empirical data were collected from Lake Puulavesi, an oligotrophic lake located in
207 Central Finland. Its areal coverage is approximately 330 km², with an average depth of
208 9.2 m and the deepest part reaching 62 m. The samples for vendace age and growth
209 determination were collected from different basins of Lake Puulavesi between 1977 and
210 2017. The model is based on empirically observed growth trajectories (total N = 93,
211 female N = 62, male N = 31). The age was determined from the annuli of vendace
212 scales located below pelvic fins. The radius of the entire scale (S) and the radius from
213 scale focus to the annulus i (S_i) were measured from the anterior part of the scale that
214 was magnified (20–40 x) using a microfiche reader. The ages were as follows: 3-year-
215 olds N = 34; 4-year-olds N = 20; 5-year-olds N = 37; and 6-year-olds N = 2. Because
216 the length at age was back-calculated, the older the fish, the more information it
217 provided from the previous years. Vendace is known to reach maturity usually on their
218 second autumn, so it was here assumed that all the specimens were mature. The back-
219 calculation of length at age (L_t) of each individual was done using the Monastyrky's
220 equation $L_t = L \times \left(\frac{s_t}{s} \right)^b$ (Monastyrsky 1930), where L = the measured total length when
221 the fish was caught, s_t = the width of annulus at age t, S = radius of the entire scale,
222 and b = 0.641. The value of 0.641 for the exponent b is an estimate from several
223 Finnish vendace stocks (Marjomäki and Huolila 2001).

224 The empirically collected weight data ($N = 27$) and the growth trajectories calculated
225 above were used to calculate the length–weight relationship $W = a \times L^b$ (Ricker 1975).
226 In this equation W = fresh weight in grams (precision 0.1 g) and L = length in cm
227 (precision 1 mm). The parameter a (scaling coefficient for the weight at length of the
228 fish) the parameter b (shape parameter for the body form of the species) were
229 calculated to be $a = 0.007$, and $b = 0.003$. The lengths varied between 120 and 170 mm
230 (mean 146 mm, s.d. = 8.63), and the weights varied between 12 and 27 g, (mean 18.7
231 g, s.d. = 3.7). The length – weight relationship is important because weight scales with
232 fecundity, and therefore plays a crucial role in population dynamics. In this particular
233 study, it also forms the basis that reproductive senescence is modelled on.

234 Back-calculated individual growth trajectories from Lake Puulavesi were summarised
235 using a non-linear least-squares fit of the vB growth equation which was fit for our data
236 $L_t = L_\infty - (L_\infty - L_0)e^{-kt}$, where L_t = length at age t , L_∞ = asymptotic length, L_0 = length
237 at $t = 0$, and k = the intrinsic individual growth rate. The association between the vB
238 parameters L_∞ and k was estimated using an empirically based linear regression model
239 which yielded the following fit: $\ln(k) = 1.27 - 0.13 * L_\infty$ with residual s.d. = 0.30.

240 In the scenarios with no reproductive senescence (i.e. how most life-history and
241 fisheries models describe reproduction), fecundity was based purely on the linear
242 function for individual fecundity per gram body weight: $39.06 + 118.47 \times$ wet mass in
243 grams (Table 1) derived from empirical data (Karjalainen et al. 2016). For ease of
244 comparison against the reproductive senescent scenario, we assigned a “fecundity
245 factor” of 1 for each age group, meaning no change in fecundity with age (Table 1).

246 Karjalainen et al. (2016) showed an age-dependent decrease in gonadosomatic index
247 (GSI), a pattern that could be indicative of reproductive senescence. We used this GSI
248 as a proxy for reproductive senescence (Table 1). As we only had GSI data for fish up
249 to four years old, the GSI for 5- and 6-year-old fish was linearly extrapolated from the
250 existing data. We used linear extrapolation, because we are interested in the
251 mechanistic changes in population, and not specifically only in vendace. Instead of
252 using the absolute GSI values to describe reproductive senescence in the model, we
253 standardised the effect of reproductive senescence so that the GSI for age group 1 was
254 set to be the baseline and have a fecundity factor of 1 (i.e. no change, same as the non-
255 senescent population), and the following age groups from 2 to 6 were assigned a
256 fecundity factor proportional to that of age group 1. The fecundity factor was calculated
257 by dividing the GSI of age group 1 by the GSI of the age group in question, so for
258 instance to get the fecundity factor for age group 4 would be as follows: GSI for age
259 group 1 / GSI for age group 4. The linear function for fecundity (described above) was
260 then multiplied by the appropriate fecundity factor for each age group (Table 1) to model
261 reproductive senescence. This way, as the fish ages, its reproductive output declines
262 with age.

263 When actuarial senescence was not modelled, the natural mortality rate was coded to
264 be an age-independent constant of $M = 0.257$ in all adult age groups (Table 1).
265 To model actuarial senescence, we coded a natural mortality rate (M) that increases
266 with age. The senescence scenario was modelled so that a baseline natural mortality of
267 $M = 0.2$ was set for 2 year olds, and the added mortality rate per each age group was
268 adjusted to proportion from Marjomäki (2005) and is shown in Table 1. The difference

269 between natural mortality imposed by actuarial senescence and fishing mortality is that
270 natural mortality as a result of actuarial senescence increases with age, while the
271 fishing mortality is size-dependent.

272 To allow for a careful investigation of the resulting demographic structures, the actual
273 resulting natural mortality at the population level was scaled to be identical in all
274 scenarios. This means that the total natural mortality over time in all scenarios is the
275 same, but for populations with no actuarial senescence the mortality rate was
276 unchanged over age classes, and for the populations with actuarial senescence
277 present, the mortality increased with age. So, whether the natural mortality remained
278 unchanged over age classes or increased with age, the total natural mortality for a
279 population over time was equal, only the distribution among age classes differed.

280 An increase in natural mortality following sexual maturity and reproduction is an
281 important trade-off in life-history evolution (Kuparinen et al. 2011). To take this into
282 account, and to add biological realism in the model, a survival cost of reproduction i.e.
283 increased mortality rate after having become sexually mature was added to the natural
284 mortality rate in every scenario, for every maturing fish. The survival cost of
285 reproduction was estimated to be the increase in mortality rate from age group 1 to age
286 group 2 as per Marjomäki (2005), and this was applied once in every scenario, whether
287 actuarial or reproductive senescence was modelled or not.

288 *Simulation design*

289 The initial starting population was 2000 individuals. The population size was selected
290 due to model optimisation and plays no role in the results of the study. Each scenario

291 was then simulated for 1000 years. All populations reached a state of ecological stability
292 in approximately 600 years. One hundred ecologically and evolutionarily stable
293 populations were saved for all scenarios, and these populations were then randomly
294 sampled to be used as the starting population in further simulations.

295 Simulations were run for 500 years. The population was kept in a pristine equilibrium
296 state for 200 years before fishing was simulated for a period of 100 years. Fishing
297 started in year 200 and ceased in year 300, and populations were then allowed to
298 recover for 200 years. Vendace is traditionally fished by seining and trawling, which
299 means that the retention probability increases with the size of the fish to a certain size
300 and is constant after that. To mimic seining or trawling selection and to describe length-
301 dependent gear selectivity in the population, we used a logistic curve $r(l) =$

302 $\left(\frac{\exp(a+bl)}{1+\exp(a+bl)} \right)$, where $r(l)$ = the retention probability of a fish of length l , and $a = -9$ and
303 $b = 0.85$ are shape parameters, so that 50% retention probability is reached at length –
304 a/b (Kuparinen et al. 2009). We also ran separate simulations for gill net fishing by

305 describing a dome-shaped selectivity curve $r(l) \sim \exp\left(-\frac{(l-\mu)^2}{2\sigma^2}\right)$, where $r(l)$ = the
306 retention probability of a fish of length l , $\mu = 12$ (fish length in cm at which the selection
307 curve peaks), and $\sigma = 0.5$ (standard deviation describing the width of the curve around
308 its peak). For simplicity hereafter, when we discuss trawling, a logistic selection curve is
309 assumed, and when we discuss gillnetting, a dome-shaped selection curve is assumed.
310 Regardless of the fishing method, the fishing mortality (F) of the fully selected size class
311 was set to 0.7, which is considered a realistic level of magnitude for intensively fished
312 populations (Viljanen 1986). The fishing mortality in terms of biomass was kept identical

313 for the senescent and non-senescent scenarios. All scenarios were explored across
314 pristine, harvest and recovery periods over 500 years. We created 100 independent
315 replicates for each scenario.

316 All simulations and analyses were conducted using R version 1.1.456 (R Core Team,
317 2018).

318 **Results**

319 Populations in all scenarios had reached an equilibrium and therefore showed only
320 minor temporal fluctuations in any of the population parameters before fishing
321 commenced in year 200. However, scenarios including actuarial senescence
322 consistently differed from those that did not include actuarial senescence. These
323 differences were seen before, during and after fishing in all parameters investigated.
324 Given that actuarial senescence appeared to be the major cause of the differences (Fig.
325 2), likely due to the relatively low reduction in reproductive output with age (Fig. S1, S2),
326 we focus most of the present work on two instead of four scenarios: a scenario with
327 both reproductive and actuarial senescence and a scenario with no senescence.
328 Additionally, reproductive and actuarial senescence are known to be linked (Kirkwood
329 and Shanley 2010), so exploring either both types of senescence together or none at all
330 is biologically more relevant than separating the senescence types.

331 ***Asymptotic length***

332 The populations with senescence had a consistently lower L_∞ than those with no
333 senescence. For both the senescent and non-senescent scenarios, fishing caused a
334 decline in L_∞ (Fig. 3a, b), and the decline caused by trawling was larger than the decline

335 caused by gillnetting, regardless of the presence of senescence. However, the type of
336 fishing played a role in the relative change within a scenario. The senescent scenario had
337 a smaller decline in L_{∞} than the non-senescent scenario when trawled (Fig. 4a). The
338 opposite occurred when gillnetting was applied: the senescent scenario had a larger drop
339 in L_{∞} as a result of dome-shaped fishing compared to the non-senescent scenario (Fig.
340 4b). When fishing was ceased after 100 years, L_{∞} started to increase slowly in all
341 scenarios, but in none of the scenarios did the L_{∞} recover back to the level prior to fishing.
342 Associated changes in the vB growth parameter k , and average size and age at
343 maturation are shown in supplementary material (Fig S3 a, b, c, d, respectively).

344 *Biomass*

345 In the absence of fishing, whether pristine or recovery phase, the scenario with
346 senescence produced a lower biomass than the scenario without senescence (Fig. 3c,
347 d). When fishing pressure was applied the biomass of both populations declined.
348 Trawling (Fig. 3c) caused a larger drop than gillnetting (Fig. 3d). However, when
349 trawled, the population with senescence maintained a higher biomass than the one
350 without senescence (Fig. 3c). In the gillnetting scenario, the senescent population had a
351 slightly lower biomass during fishing compared to the non-senescent population (Fig.
352 3d).

353 Regardless of the type of fishing, the relative drop in biomass for populations with
354 senescence was smaller than for those with no senescence (Fig. 4 c, d). When trawling
355 was applied, the level of biomass stayed relatively constant for both senescent and non-
356 senescent scenarios (Fig. 4c). However, gillnetting caused a sharp decline in biomass
357 then a sharp increase and then a slow, continuous decline for both scenarios (Fig. 4d).

358 The decline did not level off at any point during hundred years of fishing. When fishing
359 was ceased, all scenarios experienced a rapid increase in biomass with an initial peak
360 (that exceeded the level prior to fishing in gillnetting scenario), and then a sharp drop.
361 These peaks and drops were larger in the gillnetting scenario compared to the trawling
362 scenario. While all scenarios eventually settled to little variation and a slow, increasing
363 trend, in two hundred years of recovery, no population had recovered to the pre-fishing
364 levels.

365 *Number of fish*

366 The number of individuals (N) was consistently higher for populations with senescence,
367 than for those without, regardless of fishing type or the presence or absence of fishing
368 (Fig. 3e, f). The start of trawling caused a rapid initial decline in the number of fish, but
369 as trawling continued, the N increased in both senescent and non-senescent scenarios,
370 however it never reached the pre-fishing level (Fig. 3e). This was different from
371 gillnetting, which caused a steady increase in the N during fishing, above the pre-fishing
372 levels (Fig. 3f). As fishing was ceased, the populations that were trawled experienced a
373 rapid initial increase in N , and then a declining trend. When gillnetting was ceased, it
374 caused a slow decline in the number of fish. No scenario reached the pre-fishing level in
375 two hundred years of recovery.

376 In both trawling and gillnetting scenarios, the relative change in the number of fish was
377 smaller for the senescent scenario, compared to the non-senescent scenario (Fig. 4e,
378 f). However, as the fishing continued, the difference between the senescent and non-
379 senescent scenarios declined.

380 **Discussion**

381 Many collapsed fish populations have not recovered even after significant reductions in
382 fishing pressure, or are recovering slower than expected (Hutchings and Reynolds
383 2004). Our individual-based eco-evolutionary simulations shed light on how
384 reproductive and actuarial senescence affect fish population dynamics under different
385 fishing selection regimes. Populations with senescence evolved to have a lower L_∞ , and
386 during fishing the L_∞ declined further. However, the senescent and non-senescent
387 populations responded differently to different fishing selection regimes: when fishing by
388 trawling (described by a logistic selection curve), the relative decline in L_∞ in the
389 senescent population was less than in the non-senescent population. When fishing by
390 gillnet (described by a dome-shaped selection regime), the opposite occurred, and the
391 senescent population experienced a proportionately larger decline in L_∞ . The effect of
392 senescence on population dynamics in terms of biomass and number of fish appeared
393 to be density dependent. When the population was relaxed from strong density
394 dependency during trawling, populations with senescence maintained a higher biomass
395 and had a higher N than populations with no senescence present. When gillnetting was
396 applied, the senescent population maintained higher numbers, but the total biomass
397 was lower than the non-senescent population's biomass. Given the sensitivity of
398 fisheries models to the mass-fecundity relationship and total mortality rates, and the
399 common practice of relying on the reproductive effort of old, large individuals, these
400 results draw attention to the importance of considering senescence as a life-history trait
401 affecting population dynamics and recovery.

402 *Asymptotic length*

403 Populations experiencing senescence evolved to have smaller asymptotic length and
404 coupled with this was a higher intrinsic growth rate, and smaller size and younger age at
405 maturation. These trends were present both when there was no fishing and therefore
406 density-dependent processes regulated the population size, and when fishing had
407 relaxed the population from strong density-dependent competition. Both extrinsic
408 mortality (fishing) and intrinsic mortality (actuarial senescence) led to a declining
409 asymptotic length. This may indicate the presence of a trade-off between increased
410 investment in growth and/ or reproduction early in life (as asymptotic length was
411 associated with earlier reproduction and higher growth rate) and decreased survival
412 later in life. The well-known effects of fishing-induced evolution i.e. selection toward
413 smaller size, smaller size at maturation, and higher growth rate (Heino et al. 2015;
414 Hunter et al. 2015; Uusi-Heikkilä et al. 2015) may therefore enhance the trade-offs
415 associated with senescence and the evolution of life-history traits. Additionally, if
416 increased allocation of resources to reproduction early in life is associated with
417 decreased survival later in life (Kirkwood and Rose 1991), fishing-induced evolution
418 may be indirectly promoting the evolution of senescence through selecting for smaller
419 size and age at maturity.

420 An interesting effect was seen in the response of senescent and non-senescent fish to
421 different fishing methods when comparing the pristine, fishing, and recovery phases
422 within scenarios. Trawling caused a larger absolute decline in asymptotic length (Fig.
423 3a) than did gillnetting (Fig. 3b) for both senescent and non-senescent populations.
424 However, in the trawling scenario the asymptotic length of the senescent population
425 declined proportionately less than that of the non-senescent population (Fig. 4a). The

426 opposite occurred in the gillnetting scenario (Fig. 4b), where the asymptotic length of
427 the senescent population declined proportionately more from the pristine phase to the
428 fishing phase compared to the non-senescent population. In the 200 years of recovery,
429 the recovery rates of asymptotic length in senescent and non-senescent populations
430 also varied. The different response of senescent and non-senescent fish to different
431 fishing methods is an important notion, as the presence or absence of senescence can
432 affect the magnitude of the change in lifehistory traits in response to fishing. Further, the
433 change in lifehistory characters directly and indirectly affects the population level
434 response.

435 *Population level consequences of senescence*

436 The changes in asymptotic length, and associated changes in growth rate, and size and
437 age at maturity translated to changes in population level variables. As the carrying
438 capacity of both senescent and non-senescent populations were the same, and the
439 asymptotic length of the fish decreased as a result of senescence and/ or fishing, the
440 senescent population could contain a higher number of fish through pristine, fishing and
441 recovery phases. However, the response of the senescent and non-senescent
442 populations in terms of biomass differed during fishing, and the type of fishing affected
443 the response.

444 In absolute terms, the senescent population maintained a higher biomass during
445 trawling than the non-senescent population (Fig. 3c). Our simulation allowed for control
446 over the fishing mortality, and the catch in terms of biomass was set identical for the
447 senescent and non-senescent populations. Before the fishing started, the population
448 with senescence had a lower biomass than that of the non-senescent population. Since

449 the absolute biomass of the catch is the same in both populations, this means that the
450 proportional catch from the senescent population (with initially lower biomass) is higher
451 than the catch from the non-senescent population (which had a higher biomass initially).
452 Therefore, the lower asymptotic length of the senescent population (Fig. 3a) did not lead
453 to them being less likely to get caught, but indeed the opposite. Regardless of being
454 more likely to get caught, the senescent population maintained a higher number and
455 higher biomass than the non-senescent population. The explanation for the higher
456 biomass and the higher number of senescent population compared to the non-
457 senescent population is likely in the lifehistory trade-offs. The population with
458 senescence has evolved to have a lower asymptotic length and therefore they mature
459 and start reproducing younger and at a smaller size. Fishing as a source of external
460 mortality pushes the age and size at maturity even younger and smaller, so the higher
461 biomass and number of fish is likely maintained by this earlier reproduction and not
462 lesser fishing mortality. This is an important notion, as management practices tend to
463 focus on saving the big fish (Birkeland and Dayton 2005; Barneche et al. 2018). While
464 we do not deny the importance of big fish, we wish to draw attention to the important
465 contribution that smaller fish can have in population recovery, especially in extensively
466 exploited populations.

467 Gillnetting presents a different kind of selection curve than trawling. While the logistic
468 selection curve of trawling allows virtually no escapement of the larger fishes, the dome-
469 shaped selection curve of gillnetting selects the mid-sized and allows the escapement of
470 small and large fish. This kind of selection curve leads to a less skewed population in
471 terms of size, and consequently age. As a result, the responses of senescent population

472 and the non-senescent population to gillnetting in terms of biomass did not differ as
473 much as they did to trawling. However, the drop in biomass from pristine phase to
474 fishing phase was relatively smaller for the senescent population (Fig. 4d), despite the
475 larger relative drop in asymptotic length (Fig. 4b). Like the situation in trawling scenario,
476 the enhanced reproduction of younger and smaller fish is likely to drive the relatively
477 higher biomass of the senescent population.

478 The present study showed a decline in the age and size at maturity for senescent
479 populations, and fishing enhanced this trend further. However, the changes (or the
480 direction of the change) in life-history traits as a result of fishing depend on many factors
481 including species, fishing effort, and environmental conditions. In their meta-analysis,
482 Rochet (1998) controlled for the effect of phylogeny and showed on 77 stocks that
483 fishing induced a decline in age at maturity but an increase in size at maturity. If this
484 were to occur in addition to senescence, it could be speculated that this would likely
485 lead to similar results than in the present study: younger age but larger size at
486 reproduction would probably mean that the reproductive output is even higher if
487 fecundity is assumed to scale isometrically with body size, as most lifehistory and
488 fisheries models do, thereby highlighting the role of young individuals in population
489 recovery even more. However, the increased density of young fish may eventually lead
490 to higher density dependent mortality at younger age classes, or decline in food
491 availability, which could indirectly affect recruitment (Abrams and Rowe 1996). More
492 studies are needed to understand the recruitment dynamics under different density
493 scenarios.

494 While the asymptotic length of senescent and non-senescent fish responds to different
495 fishing selection regimes differently, the population level consequences of senescence
496 might be partially density dependent (Graves and Mueller 1993). During high external
497 mortality it might be better to invest in reproduction rather than grow large. In other
498 words, given that senescent fish are smaller to start with, senescence may buffer the
499 population against high external mortality by pushing for earlier reproduction. Indeed,
500 looking at the other side of the coin, high rate of external mortality is expected to
501 accelerate the rate of senescence (Williams 1957) and as a trade-off potentially select
502 for earlier reproduction.

503 The density-dependent consequences of senescence can be seen when the effects of
504 reproductive and actuarial senescence are teased apart (Fig. 2). While the populations
505 with actuarial and reproductive senescence have lower asymptotic length before fishing
506 pressure is applied, under fishing pressure this population maintains higher asymptotic
507 length than a population with actuarial senescence only. This suggests that during high
508 external mortality, if the population experiences both types of senescence (actuarial and
509 reproductive), then maintaining a larger body size becomes beneficial in order to
510 maximise fitness in terms of producing as many offspring as possible. On the other
511 hand, for a population with only actuarial senescence, their reproduction does not suffer
512 in terms of declining GSI with age, so therefore smaller body size carries smaller fitness
513 penalty compared to populations that experience both types of senescence.

514 *Implications to fisheries science*

515 Exploitation and over-exploitation are major causes for the decline of fisheries (Perissi
516 et al. 2017) and even extinction of fish populations (Dulvy et al. 2003b). The traditional

517 density-dependent population growth theory suggests that at low abundance
518 populations should grow at a fast rate. Following this, fish stocks should recover quickly
519 after fishing has been ceased. Yet, despite large-scale fishing moratoriums, many fish
520 stocks have not fully recovered from intense fishing and remain low (Myers and
521 Barrowman 1997; Bailey 2011; Rougier et al. 2012; Pedersen et al. 2017), or are
522 recovering at a lower rate than expected (Hutchings and Reynolds 2004). While the
523 reasons behind the lack of recovery are complex, the failure of fishing moratoriums to
524 result in stock recovery warrants a closer investigation at the life-history evolution and
525 trade-off in fish, and the potential demographic consequences thereof.

526 Based on the evidence for the presence of senescence in fish (Gerking 1957; Comfort
527 1960, 1963; Woodhead and Ellett 1966, 1967, 1969a, b; Patnaik et al. 1994; Woodhead
528 1998; Beverton et al. 2004; Reznick et al. 2006; Hendry et al. 2004; Reznick et al. 2004;
529 Morbey et al. 2005; Carlson et al. 2007; Terzibasi Tozzini et al. 2013; Uriarte et al.
530 2016; Benoît et al. 2018), taking senescence into consideration in fisheries stock
531 assessments could improve the accuracy of stock assessment and success in
532 management. As described by Le Bris *et al.* (2015), fisheries models that predict
533 population dynamics often assume that individual fecundity increases with the
534 increasing size of fish. These models are particularly sensitive to variations in the
535 fecundity–mass relationship (Le Bris et al. 2015). Therefore, for species that undergo
536 senescence, estimates of fecundity that ignore senescence may prove to be incorrect.
537 As discussed above, the smaller and younger fish may have an important role in
538 population recovery.

539 Similarly, due to lack of age-specific natural mortality data, typical fisheries models
540 assume a constant rate of natural mortality regardless of the age and size of the fish, or
541 a rate of natural mortality that scales with body size raised to a negative power
542 (summarised in Gislason *et al.*, 2010), thereby assuming a decreased rate of natural
543 mortality as the individual grows and ages. For species experiencing senescence,
544 ignoring changes in natural mortality with age could lead to unrealistically low mortality
545 estimates. Additionally, it could mask the importance of young individuals in population
546 recovery, hindering our management efforts further. Recruitment and natural mortality
547 are the basic building blocks of stock assessment, and therefore ignoring the ways that
548 senescence can change them could lead to biased estimates of fish population sizes.
549 Inaccuracies in stock assessment models, whether related to reproductive capacity or
550 mortality rates, may risk the sustainability of fishing.

551 Importantly, the practice of conserving old and large individuals (Birkeland and Dayton
552 2005), may not be sufficient, and could even be harmful if senescence is indeed widely
553 present in fishes. While old and large individuals have important functions in the wider
554 ecosystem as predators (Petchey *et al.* 2008), trainers of young ones in migration and
555 feeding (Petitgas *et al.* 2010), and in contributing to the gene pool (Uusi-Heikkilä *et al.*
556 2015), their role in maintaining population resiliency through recruitment may not be as
557 pivotal as is thought. On the one hand, this may be because if senescence is widely
558 present in fishes, then relying on large individuals could be misleading if their natural
559 mortality is higher than estimated, and their reproductive output is lower than estimated.
560 On the other hand, it may be because we are under-estimating the role of smaller and
561 younger individuals and their reproductive capacity. Early life reproduction may be an

562 important contributor to population resiliency and recovery, perhaps more so than late
563 life reproduction.

564 Senescence can mask changes in life-history responses to fishing. As demonstrated in
565 the present study, the presence or absence of senescence affects how the population
566 responds to different fishing selections regimes: while trawling reduced the asymptotic
567 length of non-senescent population more, gillnetting reduced the asymptotic length of
568 the senescent population more. Depending on the fishing method in question, the
569 magnitude of change in life-history characters may be higher or lower than anticipated if
570 senescence is present. As a result, the population level response will change too.
571 Failure to consider senescence as a fish life-history trait with trade-offs and population
572 level consequences will hinder our progress in understanding fish population resiliency.

573

574

575

576

577

578

579

580

581

582 **Declarations**

583 The authors thank Markku Raatikainen for vendace age determination. This work was
584 supported by funding from the Emil Aaltonen Foundation (PAA), the Academy of
585 Finland grant no. 317495 (AK), and grant no. 325107 (SUH), Discovery Grant from the
586 National Sciences and Engineering Research Council of Canada NSERC (AK), the
587 European Research Council through COMPLEX-FISH 770884 (AK), the Finnish
588 Cultural Foundation (SUH). The authors also thank the Centre for Development,
589 Transport and the Environment for long-term financial support for vendace research in
590 Lake Puulavesi. The authors declare no conflicts of interest. The present study reflects
591 only the authors' view and the European Research Council is not responsible for any
592 use that may be made of the information it contains.

593

594

595

596

597

598

599

600

601

602

603

604

605

606

607

608

609

610

611

612 **References**

613 Abrams PA, Rowe L (1996) The effects of predation on the age and size of maturity of
614 prey. *Evolution (N Y)* 50:1052–1061

615 Ahti PA, Kuparinen A, Uusi-heikkilä S (2020) Size does matter — the eco-evolutionary
616 effects of changing body size in fish. *Environ Rev* 14:1–14

617 Andersen KH, Beyer JE (2015) Size structure, not metabolic scaling rules, determines
618 fisheries reference points. *Fish Fish* 16:1–22. <https://doi.org/10.1111/faf.12042>

619 Bailey KM (2011) An Empty Donut Hole: The Great Collapse of a North American
620 Fishery. *Ecol Soc* 16:. <https://doi.org/10.5751/ES-04124-160228>

- 621 Barneche DR, Robertson DR, White CR, Marshall DJ (2018) Fish reproductive-energy
622 output increases disproportionately with body size. *Science* (80-) 360:642–645
- 623 Benoît HP, Swain DP, Hutchings JA, et al (2018) Evidence for reproductive senescence
624 in a broadly distributed harvested marine fish. *Mar Ecol Prog Ser* 592:207–224.
625 <https://doi.org/10.3354/meps12532>
- 626 Beverton RJH, Hylen A, Østvedt OJ, et al (2004) Growth, maturation, and longevity of
627 maturation cohorts of Norwegian spring-spawning herring. *ICES J Mar Sci* 61:165–
628 175. <https://doi.org/10.1016/j.icesjms.2004.01.001>
- 629 Birkeland C, Dayton PK (2005) The importance in fishery management of leaving the
630 big ones. *Trends Ecol Evol* 20:3–6. <https://doi.org/10.1016/j.tree.2005.03.015>
- 631 Bonsall MB, Mangel M (2004) Life-history trade-offs and ecological dynamics in the
632 evolution of longevity. *Proc R Soc B Biol Sci* 271:1143–1150.
633 <https://doi.org/10.1098/rspb.2004.2722>
- 634 Brunel T, Ernande B, Mollet FM, Rijnsdorp AD (2013) Estimating age at maturation and
635 energy-based life-history traits from individual growth trajectories with nonlinear
636 mixed-effects models. *Oecologia* 172:631–643. <https://doi.org/10.1007/s00442-012-2527-1>
- 638 Carlson SM, Hilborn R, Hendry AP, Quinn TP (2007) Predation by bears drives
639 senescence in natural populations of salmon. *PLoS One* 2:
640 <https://doi.org/10.1371/journal.pone.0001286>
- 641 Charnov EL, Gislason H, Pope JG (2013) Evolutionary assembly rules for fish life

- 642 histories. Fish Fish 14:213–224. <https://doi.org/10.1111/j.1467-2979.2012.00467.x>
- 643 Comfort A (1960) The effect of age on growth-resumption in fish (*Lebistes*) checked by
644 food restriction. Gerontologia 4:177–186
- 645 Comfort A (1963) Effect of delayed and resumed growth on the longevity of a fish
646 (*Lebistes reticulatus*, Peters) in captivity. Gerontologia 8:150–155
- 647 Dulvy NK, Sadovy Y, Reynolds JD (2003a) Extinction vulnerability in marine populations
- 648 Dulvy NK, Yvonne S, Reynolds JD (2003b) Extinction vulnerability in marine
649 populations. Fish Fish 4:25–64. <https://doi.org/10.1046/j.1467-2979.2003.00105.x>
- 650 Enberg K, Jørgensen C, Mangel M (2010) Fishing-induced evolution and changing
651 reproductive ecology of fish: the evolution of steepness. Can J Fish Aquat Sci
652 67:1708–1719. <https://doi.org/10.1139/F10-090>
- 653 Gerking SD (1957) Evidence of aging in natural populations of fishes. Gerontologia
654 1:287–305
- 655 Gislason H, Daan N, Rice JC, Pope JG (2010) Size, growth, temperature and the
656 natural mortality of marine fish. Fish Fish 11:149–158.
657 <https://doi.org/10.1111/j.1467-2979.2009.00350.x>
- 658 Graves JL, Mueller LD (1993) Population density effects on longevity. Genetica 91:99–
659 109. <https://doi.org/10.1007/BF01435991>
- 660 Heino M, Beatriz DP, Dieckmann U (2015) Fisheries-Induced Evolution. Annu Rev Ecol
661 Evol Syst 46:461–480. <https://doi.org/10.1146/annurev-ecolsys-112414-054339>
- 662 Heino M, Kaitala V (1999) Evolution of resource allocation between growth and

- 663 reproduction in animals with indeterminate growth. *J Evol Biol* 12:423–429.
- 664 <https://doi.org/10.1046/j.1420-9101.1999.00044.x>
- 665 Hendry AP, Morbey YE, Berg OK, Wenburg JK (2004) Adaptive variation in
666 senescence: reproductive lifespan in a wild salmon population. *Proc R Soc B* 259–
667 266. <https://doi.org/10.1098/rspb.2003.2600>
- 668 Hunter A, Speirs DC, Heath MR (2015) Fishery-induced changes to age and length
669 dependent maturation schedules of three demersal fish species in the Firth of
670 Clyde. *Fish Res* 170:14–23. <https://doi.org/10.1016/j.fishres.2015.05.004>
- 671 Hutchings JA, Reynolds JD (2004) Marine fish population collapses: Consequences for
672 recovery and extinction risk. *Bioscience* 54:297–309. [https://doi.org/10.1641/0006-3568\(2004\)054](https://doi.org/10.1641/0006-3568(2004)054)
- 674 Jackson JBC (2008) Ecological extinction and evolution in the brave new ocean. *Proc*
675 *Natl Acad Sci* 105:11458–11465. <https://doi.org/10.1073/pnas.0802812105>
- 676 Jensen AL (1996) Beverton and Holt life history invariants result from optimal trade-off
677 of reproduction and survival. *Can J Fish Aquat Sci* 53:820–822.
678 <https://doi.org/10.1139/f95-233>
- 679 Jensen AL (1998) Simulation of relations among fish life history parameters with a
680 bioenergetics-based population model. *Can J Fish Aquat Sci* 55:353–357
- 681 Karjalainen J, Urpanen O, Keskinen T, et al (2016) Phenotypic plasticity in growth and
682 fecundity induced by strong population fluctuations affects reproductive traits of
683 female fish. *Ecol Evol* 6:779–790. <https://doi.org/10.1002/ece3.1936>

- 684 Kirkwood TBL, Rose MR (1991) Evolution of senescence: late survival sacrificed for
685 reproduction. *Philos Trans - R Soc London, B* 332:15–24.
686 <https://doi.org/10.1098/rstb.1991.0028>
- 687 Kirkwood TBL, Shanley DP (2010) The connections between general and reproductive
688 senescence and the evolutionary basis of menopause. *Ann N Y Acad Sci* 1204:21–
689 29. <https://doi.org/10.1111/j.1749-6632.2010.05520.x>
- 690 Kuparinen A, Hardie DC, Hutchings JA (2011) Evolutionary and ecological feedbacks of
691 the survival cost of reproduction. *Evol Appl* 5:245–255.
692 <https://doi.org/10.1111/j.1752-4571.2011.00215.x>
- 693 Kuparinen A, Kuikka S, Merilä J (2009) Estimating fisheries-induced selection:
694 Traditional gear selectivity research meets fisheries-induced evolution. *Evol Appl*
695 2:234–243. <https://doi.org/10.1111/j.1752-4571.2009.00070.x>
- 696 Le Bris A, Pershing AJ, Hernandez CM, et al (2015) Modelling the effects of variation in
697 reproductive traits on fish population resilience. *ICES J Mar Sci* 72:2590–2599
- 698 Lemaitre J-F, Gaillard J, Pemberton JM, et al (2014) Early life expenditure in sexual
699 competition is associated with increased reproductive senescence in male red
700 deer. *Proc R Soc B Biol Sci*
- 701 Lemaître JF, Berger V, Bonenfant C, et al (2015) Early-late life trade-offs and the
702 evolution of ageing in the wild. *Proc R Soc B Biol Sci* 282:.
703 <https://doi.org/10.1098/rspb.2015.0209>
- 704 Lester NP, Shuter BJ, Abrams PA (2004) Interpreting the von Bertalanffy model of

- 705 somatic growth in fishes: the cost of reproduction. Proc R Soc B Biol Sci 271:1625–
706 1631. <https://doi.org/10.1098/rspb.2004.2778>
- 707 Maklakov AA, Chapman T (2019) Evolution of ageing as a tangle of trade-offs: energy
708 versus function. Proc R Soc B Biol Sci 286:20191604.
709 <https://doi.org/10.1098/rspb.2019.1604>
- 710 Marjomäki TJ (2005) Evaluation of different harvest strategies for a vendace population
711 with highly variable recruitment: A simulation approach. Boreal Environ Res
712 10:255–273
- 713 Marjomäki TJ, Huolila M (2001) Long-term dynamics of pelagic fish density and
714 vendace (*Coregonus albula* (L.)) stocks in four zones of a lake differing in trawling
715 intensity. Ecol Freshw Fish 10:65–74. <https://doi.org/10.1034/j.1600-0633.2001.100201.x>
- 717 Marjomäki TJ, Urpanen O, Karjalainen J (2014) Two-year cyclicity in recruitment of a
718 fish population is driven by an inter-stage effect. Popul Ecol 56:513–526.
719 <https://doi.org/10.1007/s10144-014-0439-0>
- 720 Merino G, Barange M, Blanchard JL, et al (2012) Can marine fisheries and aquaculture
721 meet fish demand from a growing human population in a changing climate? Glob
722 Environ Chang 22:795–806. <https://doi.org/10.1016/j.gloenvcha.2012.03.003>
- 723 Monaghan P, Charmantier A, Nussey DH, Ricklefs RE (2008) The evolutionary ecology
724 of senescence. Funct Ecol 22:371–378. <https://doi.org/10.1111/j.1365-2435.2008.01418.x>

- 726 Monastyrsky GN (1930) O metodakh opredeleniya lineinogo rosta po cheshue ryb
727 (methods of determining the growth of fish in length by their scales). Tr Nauch Ryb
728 Khozy 5:5–44
- 729 Morbey YE, Brassil CE, Hendry AP (2005) Rapid Senescence in Pacific Salmon. Am
730 Nat 166:556–568. <https://doi.org/10.1086/491720>
- 731 Mousseau TA, Roff DA (1987) Natural selection and the heritability of fitness
732 components. Heredity (Edinb) 59:181–197. <https://doi.org/10.1038/hdy.1987.113>
- 733 Myers RA, Barrowman JAHNJ (1997) Why do Fish Stocks Collapse? The Example of
734 Cod in Atlantic Canada. Ecol Appl 7:91–106
- 735 Nussey DH, Froy H, Lemaître JF, et al (2013) Senescence in natural populations of
736 animals: Widespread evidence and its implications for bio-gerontology. Ageing Res
737 Rev 12:214–225. <https://doi.org/10.1016/j.arr.2012.07.004>
- 738 Olsen EM, Carlson SM, Gjøsæter J, Stenseth NC (2009) Nine decades of decreasing
739 phenotypic variability in Atlantic cod. Ecol Lett 12:622–631.
740 <https://doi.org/10.1111/j.1461-0248.2009.01311.x>
- 741 Patnaik BK, Mahapatro N, Jena BS (1994) Ageing in fishes. Gerontology 40:113–132.
742 <https://doi.org/10.1159/000213582>
- 743 Pedersen EJ, Link H, Thompson PL, et al (2017) Signatures of the collapse and
744 incipient recovery of an overexploited marine ecosystem. R Soc Open Sci
745 4:170215. <https://doi.org/10.1098/rsos.170215>
- 746 Perissi I, Bardi U, Bardi U, Lavacchi A (2017) Dynamic patterns of overexploitation in

- 747 fisheries. *Ecol Modell* 359:285–292.
- 748 <https://doi.org/10.1016/j.ecolmodel.2017.06.009>
- 749 Petchey OL, Beckerman AP, Riede JO, Warren PH (2008) Size, foraging, and food web
750 structure. *Proc Natl Acad Sci* 105:4191–4196.
- 751 <https://doi.org/10.1073/pnas.0710672105>
- 752 Petitgas P, Secor DH, McQuinn I, et al (2010) Stock collapses and their recovery:
753 mechanisms that establish and maintain life-cycle closure in space and time. *ICES*
754 *J Mar Sci* 67:1841–1848
- 755 Quince C, Abrams PA, Shuter BJ, Lester NP (2008) Biphasic growth in fish I :
756 Theoretical foundations. *J Theor Biol* 254:197–206.
757 <https://doi.org/10.1016/j.jtbi.2008.05.029>
- 758 Reznick D, Bryant M, Holmes D (2006) The evolution of senescence and post-
759 reproductive lifespan in guppies (*Poecilia reticulata*). *PLoS Biol* 4:0136–0143.
760 <https://doi.org/10.1371/journal.pbio.0040007>
- 761 Reznick D, Ghalambor C, Nunney L (2002) The evolution of senescence in fish. *Mech*
762 *Ageing Dev* 123:773–789. [https://doi.org/10.1016/S0047-6374\(01\)00423-7](https://doi.org/10.1016/S0047-6374(01)00423-7)
- 763 Reznick DN, Bryant MJ, Roff D, et al (2004) Effect of extrinsic mortality on the evolution
764 of senescence in guppies. *Nature* 431:1095–1099.
765 <https://doi.org/10.1038/nature03042>. Published
- 766 Ricker WE (1975) Computation and interpretation of biological statistics of fish
767 populations. *Bull Fish Res Board Canada* 401. <https://doi.org/10.1038/108070b0>

- 768 Rochet M-J (1998) Short-term effects of fishing on life history traits of fishes. ICES J
769 Mar Sci 55:371–391
- 770 Rougier T, Lambert P, Drouineau H, et al (2012) Collapse of allis shad, *Alosa alosa*, in
771 the Gironde system (southwest France): environmental change, fishing mortality, or
772 Allee effect? ICES J Mar Sci 69:1802–1811
- 773 Selman C, Blount JD, Nussey DH, Speakman JR (2012) Oxidative damage, ageing,
774 and life-history evolution: Where now? Trends Ecol Evol 27:570–577.
775 <https://doi.org/10.1016/j.tree.2012.06.006>
- 776 Terzibasi Tozzini E, Dorn A, Ng’Oma E, et al (2013) Parallel evolution of senescence in
777 annual fishes in response to extrinsic mortality. BMC Evol Biol 13:.
778 <https://doi.org/10.1186/1471-2148-13-77>
- 779 Uriarte A, Ibaibarriaga L, Pawlowski L, et al (2016) Assessing natural mortality of Bay of
780 Biscay anchovy from. 234:216–234
- 781 Uusi-Heikkilä S, Whiteley AR, Kuparinen A, et al (2015) The evolutionary legacy of size-
782 selective harvesting extends from genes to populations. Evol Appl 8:597–620.
783 <https://doi.org/10.1111/eva.12268>
- 784 von Bertalanffy L (1949) Problems of organic growth. Nature 163:156–158
- 785 von Bertalanffy L (1938) A quantitative theory of organic growth (Inquiries on growth
786 laws. II). Hum Biol 10:181–213
- 787 Williams GC (1957) Pleiotropy, Natural Selection, and the Evolution of Senescence.
788 Evolution (N Y) 11:398–411. <https://doi.org/10.2307/2406060>

- 789 Woodhead AD (1998) Aging, the fishy side: An appreciation of Alex Comfort's studies.
- 790 Experiemntal Gerontol 33:39–51
- 791 Woodhead AD, Ellett S (1969a) Aspects of ageing in the guppy, *Lebistes reticulatus*
- 792 (Peters)-IV The ovary. Exp Gerontol 4:197–205
- 793 Woodhead AD, Ellett S (1969b) Endocrine aspects of ageing in the guppy, *Lebistes*
- 794 *reticulatus* (Peters) III. The testis. Exp Gerontol 4:17–25
- 795 Woodhead AD, Ellett S (1966) Endocrine aspects of ageing in the guppy, *Lebistes*
- 796 *reticulatus* (Peters) I. The thyroid gland. Exp Gerontol 1:315–330
- 797 Woodhead AD, Ellett S (1967) Endocrine aspects of ageing in the guppy, *Lebistes*
- 798 *reticulatus* (Peters) II. The interrenal gland. Exp Gerontol 2:159–171
- 799 Zhang Y, Hood WR (2016) Current versus future reproduction and longevity: a re-
- 800 evaluation of predictions and mechanisms. J Exp Biol 219:3177–3189.
- 801 <https://doi.org/10.1242/jeb.132183>
- 802 Zimmermann F, Jørgensen C (2015) Bioeconomic consequences of fishing-induced
- 803 evolution: a model predicts limited impact on net present value. Can J Fish Aquat
- 804 Sci 72:612–624. <https://doi.org/10.1139/cjfas-2014-0006>
- 805 R Core Team (2018). R: A language and environment for statistical computing. R
- 806 Foundation for Statistical Computing, Vienna, Austria. URL
- 807 <https://www.R-project.org/>.
- 808
- 809 Roff, D. A. 2002. Life History Evolution. Sinauer, Sunderland, MA.

- 810 Kirkwood. T.B.L 1977. Evolution of ageing. *Nature* 270: 301-304.
- 811 Medawar, P.B., 1952. An Unsolved Problem of Biology. Lewis, London.
- 812 R. J. H. Beverton, S. J. Holt, *On the Dynamics of Exploited Fish Populations* (Fishery
813 Investigations Series II, Her Majesty's Stationery Office, London, 1957), vol. 19.
- 814 D. A. Roff, An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.*
815
816 **40**, 1395–1404 (1983). doi:10.1139/f83-161
- 817 Marjomäki and Huolila M. (1994): Yield, stock fluctuation, total mortality and growth of
818 Lake Puulavesi vendace (*Coregonus ølbula* (L.)) in 1984-1992. - Jyväskylän yliopiston
819 biologian laitoksen tiedonantoja 68: 37 - 66. [Finnish, Engl. summary]
- 820 Carey, J.R., Judge, D.S., 2000. Longevity Records: Lifespans of Mammals, Birds,
821 Amphibians, Reptiles, and Fish. Odense University Press, Odense, Denmark.
- 822 Viljanen M. 1986: Biology, propagation, exploitation and management of vendace
823 (*Coregonus albula* L.) ín Finland. -Arch. hydrobiol. Beih. Ergebn. Limnol. 22: 73-97.
- 824 Jurvelius, J., 1991. Distribution and density of pelagic fish stocks, especially vendace
825 (*Coregonus albula* (L.)), monitored by hydroacoustics in shallow and deep southern
826 boreal lakes. *Finnish Fish. Res.* 12: 45–63.
- 827 Järvi, T. H., 1920. Die *kleine Maräne*, *Coregonus albula* L., in *Keitelesee*. *Annales
828 Acad. scient. Fennicae. Ser. A. Vol. 14*
- 829
- 830
- 831
- 832

833 **Figure legends**

834 **Fig 1.** A schematic diagram of the modelling approach. **(A)** The fish length-at-age was
835 back-calculated from fish scales. These data were then used to fit the von Bertalanffy
836 growth equation to model the L_{∞} . The L_{∞} was set to be an evolving trait so that the
837 genotype coding the L_{∞} of each individual was described by 10 diploid loci with two
838 alleles in each, one from the mother, one from the father. **(B)** The length-weight
839 relationship was specifically calculated for *C. albus* from Lake Puulavesi. Using this
840 length-weight relationship and published empirical data on egg numbers and female
841 weights (Karjalainen et al. 2016), we fitted a linear model for the fecundity-weight
842 relationship, so that as the fish body size increases, so does the egg production. **(C)**
843 The probability of a fertilised egg to hatch and the juvenile to survive until 2 years of age
844 was set to ($P = 0.002$) and the sex of the juveniles was drawn from a Bernoulli trial with
845 a probability of 0.5. **(D)** The population component describes density dependency so
846 that at 75% of the population carrying capacity, the individual growth is reduced to 50%
847 of that predicted by the individual's vB growth curve. Additionally, egg production was
848 set to be density dependent so that the closer the population was to its carrying
849 capacity, the fewer eggs were produced. **(F)** Reproductive senescence and actuarial
850 senescence are the independent variables in the model. The reproductive senescence
851 was modelled by multiplying the linear model for fecundity by the fecundity factor based
852 on the gonadosomatic index (GSI) for the year class in question. When no reproductive
853 senescence was modelled, only the linear model for fecundity was used. Actuarial
854 senescence was modelled by increasing the rate of natural mortality each year, as
855 opposed to keeping natural mortality rate constant throughout lifetime as in the scenario

856 with no actuarial senescence. (F) Equipped with the above characters, the populations
857 were then allowed to live for 500 years and traced at annual time steps. The first 200
858 years the populations lived in pristine conditions, then the populations were fished either
859 by trawling or gillnetting for 100 years, and finally the populations were allowed to
860 recover for 200 years.

861 **Fig 2.** The mean of the asymptotic length (cm) of fish over 500 years (first hundred
862 years not shown). The dashed lines denote the start (year 200) and end (year 300) of
863 fishing. The solid lines denote the asymptotic length mean in hundred replicated
864 scenarios. The black line describes a scenario with reproductive and actuarial
865 senescence, red line a scenario with actuarial senescence only, blue line a scenario
866 with no senescence, and green line a scenario with reproductive senescence only.

867

868 **Fig. 3.** Results for the (a, b) asymptotic length (cm), (c, d) biomass (units), and (e, f) the
869 number (N) of fish. In a, c, and d the fishing simulated trawling (logistic selection) and in
870 b, d and f the fishing simulated gillnetting (dome-shaped selection). The solid black
871 lines represent hundred independent replicates of the scenario with senescence, the
872 red lines represent hundred independent replicates of the scenario with no senescence
873 present. The dashed lines denote the start (year 200) and end (year 300) of fishing.

874

875 **Fig. 4.** The relative percentage change (a, b) asymptotic length (cm), (c, d) biomass
876 (units), and (e, f) the number (N) of fish. In a, c, and d the fishing simulated trawling
877 (logistic selection) and in b, d and f the fishing simulated gillnetting (dome-shaped

878 selection). The change has been scaled so that years 1 – 100 were considered as the
879 starting point and given a value of 0. Changes in all of the parameters (asymptotic
880 length, BM, N) after that are relative changes compared to years 1 – 100. The black
881 lines denote a scenario with senescence, the red lines denote a scenario without
882 senescence. The dashed lines denote the start (year 200) and end (year 300) of fishing.
883 Given the scale of the Y axis, the 95% confidence intervals are virtually invisible.

884

885 **Appendix S1.** The lifetime cumulative number of offspring in each age group during the
886 last ten years before fishing commences and the population is in equilibrium, and during
887 the last ten years of intensive fishing (after 90 years of constant fishing). The red
888 boxplots denote scenarios without senescence and black and white boxplots denote
889 scenarios with both actuarial and reproductive senescence present.

890

891 **Appendix S2.** The lifetime cumulative number of offspring in each age group during the
892 last ten years before fishing commences and the population is in equilibrium, and during
893 the last ten years of intensive fishing (after 90 years of constant fishing). The green
894 boxplots denote scenarios with reproductive senescence and blue boxplots denote
895 scenarios with actuarial senescence present.

896

897 **Appendix S3.** Results for the **(a)** asymptotic length (cm), **(b)** intrinsic growth rate k , **(c)**
898 average size (cm) at maturation, and **(d)** average age (years) at maturation over
899 hundred years (first hundred years not shown). The black lines represent hundred

900 independent replicates of the scenario with senescence, the red lines represent
901 hundred independent replicates of the scenario with no senescence present. The
902 dashed lines denote the start (year 200) and end (year 300) of fishing.

903

Figures

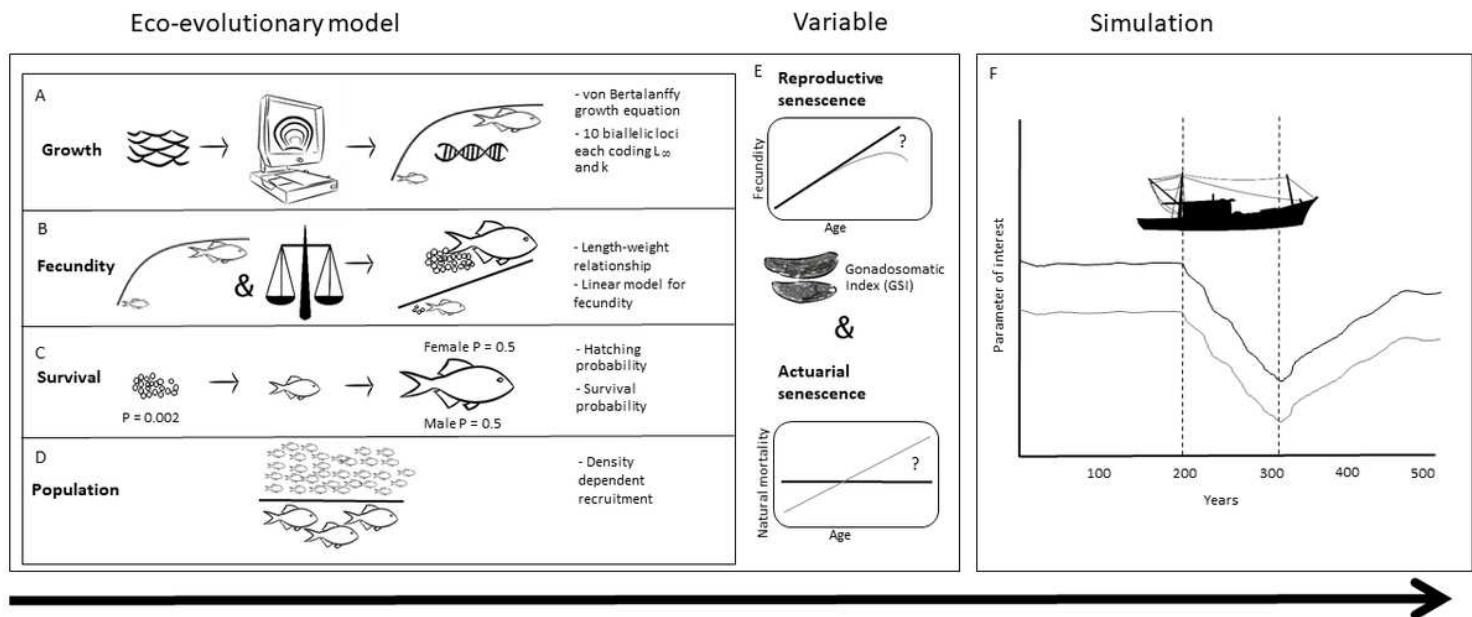


Figure 1

. A schematic diagram of the modelling approach. (A) The fish length-at-age was back-calculated from fish scales. These data were then used to fit the von Bertalanffy growth equation to model the L_{∞} . The L_{∞} was set to be an evolving trait so that the genotype coding the L_{∞} of each individual was described by 10 diploid loci with two alleles in each, one from the mother, one from the father. (B) The length-weight relationship was specifically calculated for *C. albula* from Lake Puulavesi. Using this length-weight relationship and published empirical data on egg numbers and female weights (Karjalainen et al. 2016), we fitted a linear model for the fecundity-weight relationship, so that as the fish body size increases, so does the egg production. (C) The probability of a fertilised egg to hatch and the juvenile to survive until 2 years of age was set to ($P = 0.002$) and the sex of the juveniles was drawn from a Bernoulli trial with a probability of 0.5. (D) The population component describes density dependency so that at 75% of the population carrying capacity, the individual growth is reduced to 50% of that predicted by the individual's vB growth curve. Additionally, egg production was set to be density dependent so that the closer the population was to its carrying capacity, the fewer eggs were produced. (F) Reproductive senescence and actuarial senescence are the independent variables in the model. The reproductive senescence was modelled by multiplying the linear model for fecundity by the fecundity factor based on the gonadosomatic index (GSI) for the year class in question. When no reproductive senescence was modelled, only the linear model for fecundity was used. Actuarial senescence was modelled by increasing the rate of natural mortality each year, as opposed to keeping natural mortality rate constant throughout

lifetime as in the scenario with no actuarial senescence. (F) Equipped with the above characters, the populations were then allowed to live for 500 years and traced at annual time steps. The first 200 years the populations lived in pristine conditions, then the populations were fished either by trawling or gillnetting for 100 years, and finally the populations were allowed to recover for 200 years.

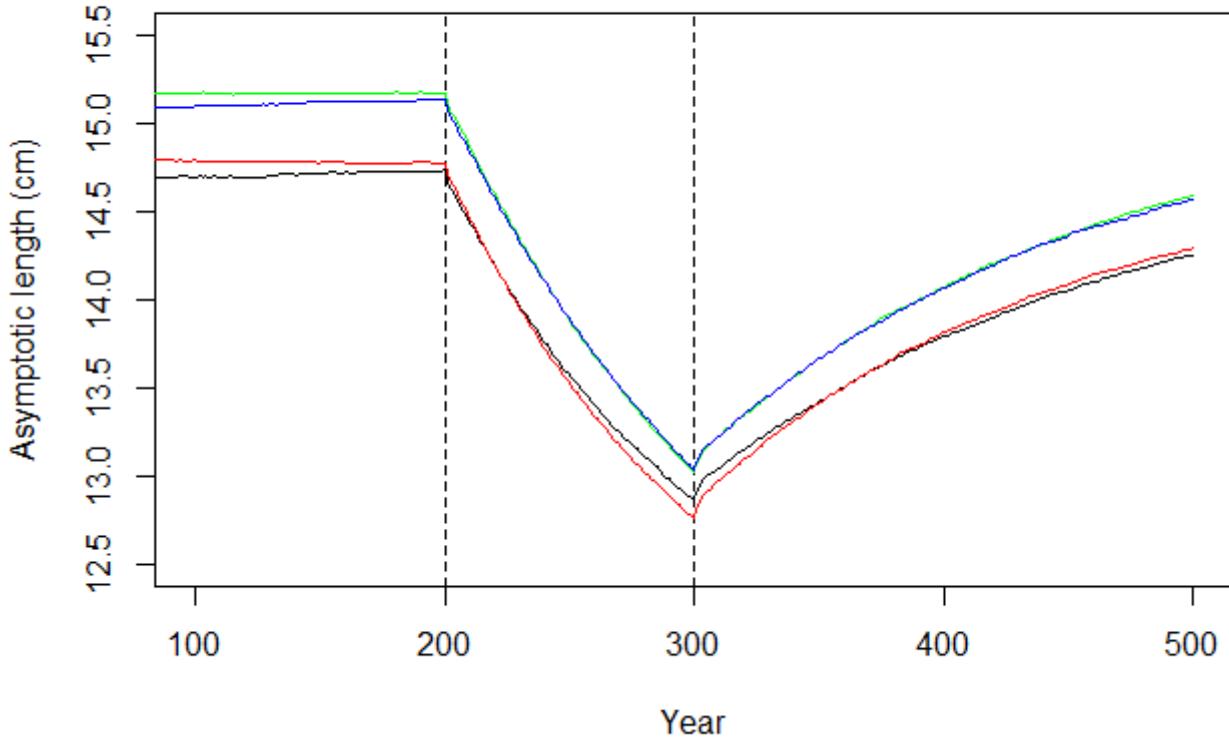


Figure 2

The mean of the asymptotic length (cm) of fish over 500 years (first hundred years not shown). The dashed lines denote the start (year 200) and end (year 300) of fishing. The solid lines denote the asymptotic length mean in hundred replicated scenarios. The black line describes a scenario with reproductive and actuarial senescence, red line a scenario with actuarial senescence only, blue line a scenario with no senescence, and green line a scenario with reproductive senescence only.

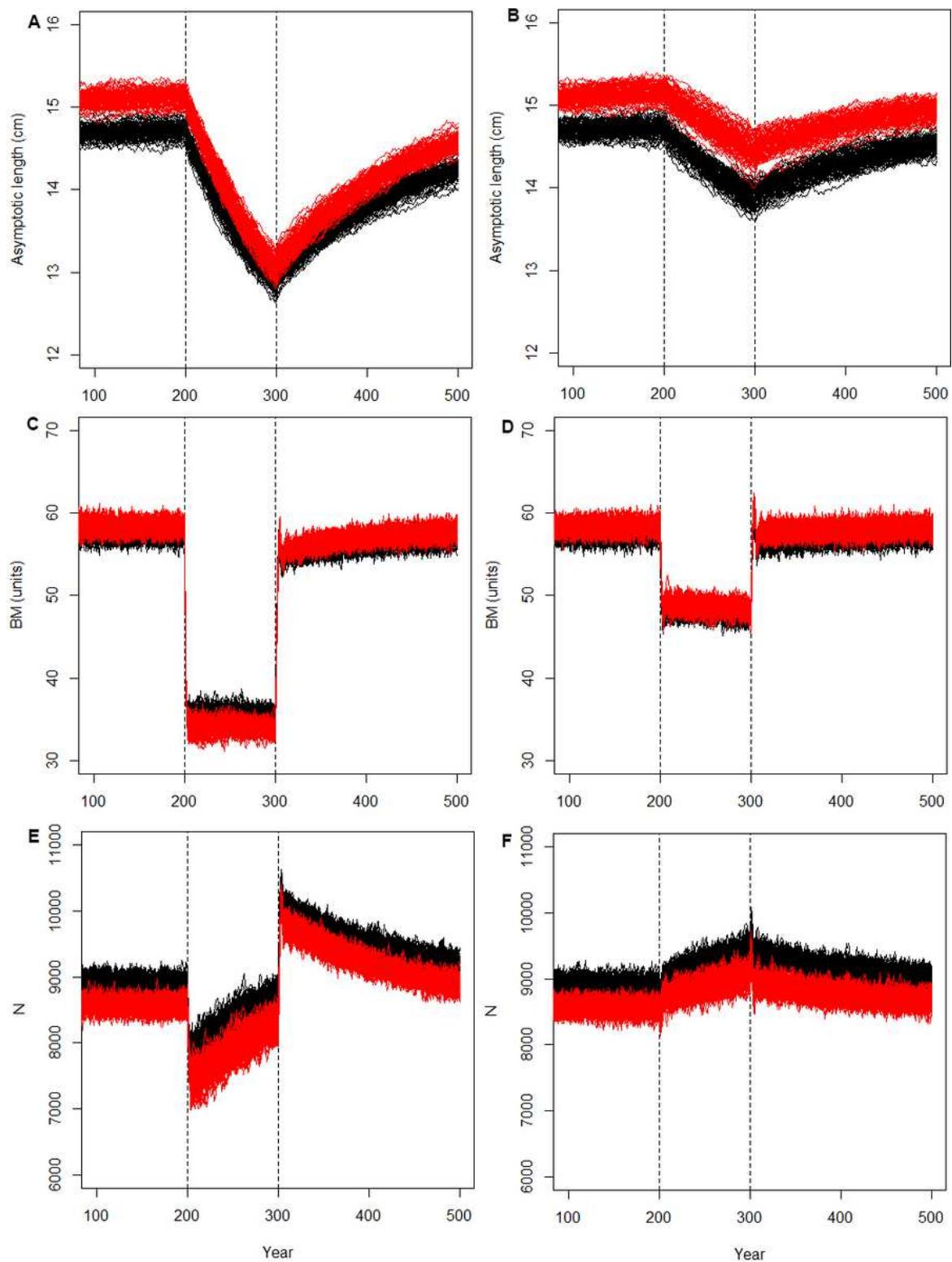


Figure 3

Results for the (a, b) asymptotic length (cm), (c, d) biomass (units), and (e, f) the number (N) of fish. In a, c, and d the fishing simulated trawling (logistic selection) and in b, d and f the fishing simulated gillnetting (dome-shaped selection). The solid black lines represent hundred independent replicates of the scenario with senescence, the red lines represent hundred independent replicates of the scenario with no senescence present. The dashed lines denote the start (year 200) and end (year 300) of fishing.

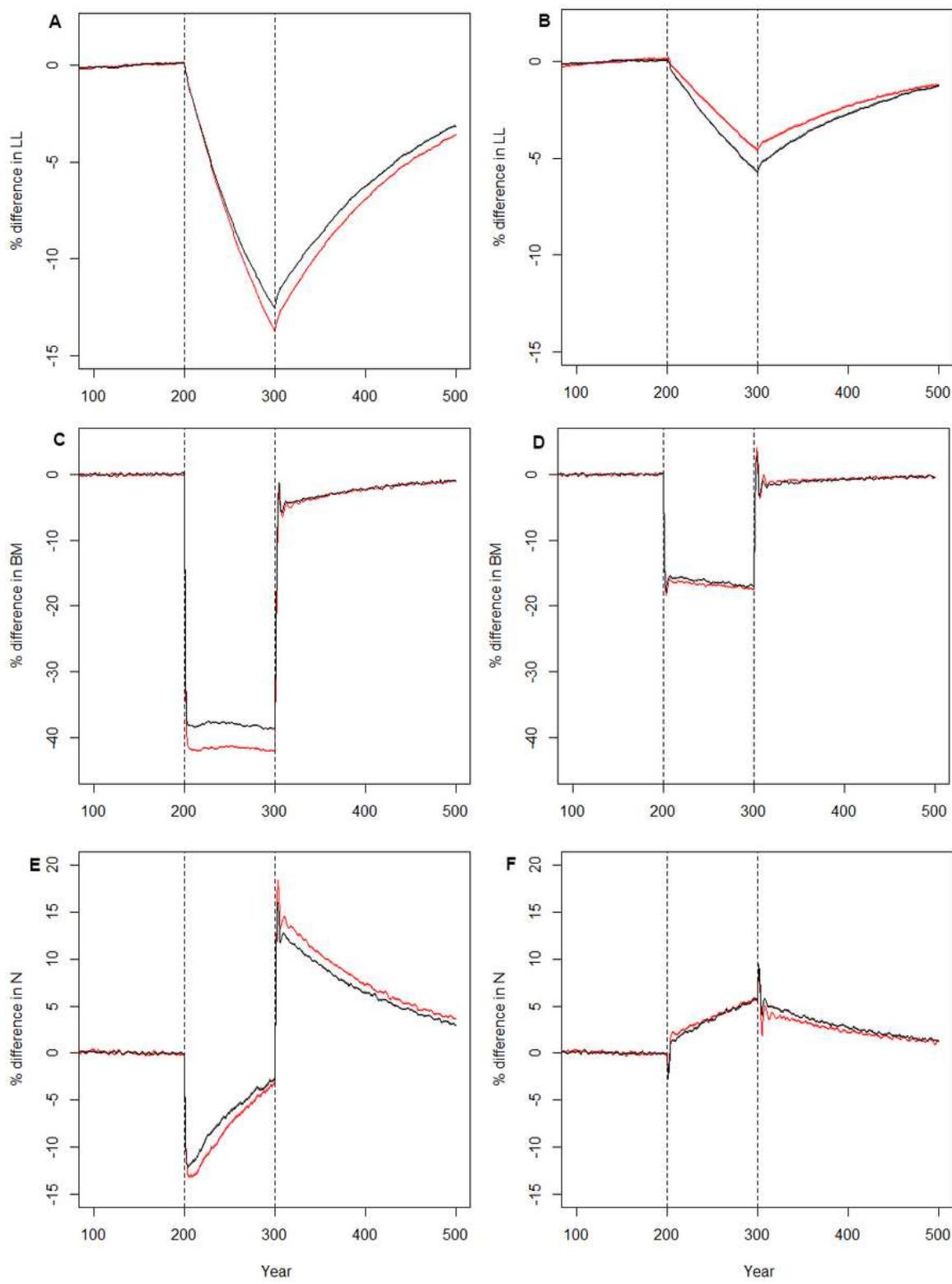


Figure 4

The relative percentage change (a, b) asymptotic length (cm), (c, d) biomass (units), and (e, f) the number (N) of fish. In a, c, and d the fishing simulated trawling (logistic selection) and in b, d and f the fishing simulated gillnetting (dome-shaped selection). The change has been scaled so that years 1 – 100 were considered as the starting point and given a value of 0. Changes in all of the parameters (asymptotic length, BM, N) after that are relative changes compared to years 1 – 100. The black lines denote a

scenario with senescence, the red lines denote a scenario without senescence. The dashed lines denote the start (year 200) and end (year 300) of fishing. Given the scale of the Y axis, the 95% confidence intervals are virtually invisible.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [S1.png](#)
- [S2.png](#)
- [S3.png](#)