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1 **Harvest-induced maturation evolution**
2 **under different life-history trade-offs and harvesting regimes**

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11 **Abstract**

12 The potential of harvesting to induce adaptive changes in exploited populations is now increa-
13 singly recognized. While early studies predicted that elevated mortalities among larger
14 individuals select for reduced maturation size, recent theoretical studies have shown condi-
15 tions under which other, more complex evolutionary responses to size-selective mortality are
16 expected. These new predictions are based on the assumption that, owing to the trade-off be-
17 tween growth and reproduction, earlier maturation implies reduced growth. Here we extend
18 these findings by analyzing a model of a harvested size-structured population in continuous
19 time, and by systematically exploring maturation evolution under all three traditionally ac-
20 knowledged costs of early maturation: reduced fecundity, reduced growth, and/or increased
21 natural mortality. We further extend this analysis to the two main types of harvest selectivity,
22 with an individual's chance of getting harvested depending on its size and/or maturity stage.
23 Surprisingly, we find that harvesting mature individuals not only favors late maturation when
24 the costs of early maturation are low, but promotes early maturation when the costs of early
25 maturation are high. To our knowledge, this study therefore is the first to show that harvesting
26 mature individuals can induce early maturation.

27 **1. Introduction**

28 Concerns over evolutionary consequences of harvesting are mounting, as both theoretical and
29 empirical studies have demonstrated the potential for rapid harvest-induced evolution (e.g.,
30 Law, 2000; Conover and Munch, 2002; Heino and Godø, 2002; Ashley et al., 2003; Coltman
31 et al., 2003; Jørgensen et al., 2007; Dieckmann et al., 2009). Life-history theory predicts that
32 increased mortality devalues life-history processes occurring later in life, relative to those oc-
33 ccurring earlier (e.g., Law 1979; Stearns, 1992; Ernande et al., 2004). Therefore, systematic
34 reductions in age and size at maturation observed for stocks exposed to heavy fishing (e.g.,
35 Jørgensen, 1990; Rijnsdorp, 1993a; Trippel, 1995) are suggestive of fisheries-induced evolu-
36 tion (e.g., Heino et al., 2002; Grift et al., 2003, 2007; Barot et al., 2004, 2005; Olsen et al.,
37 2004, 2005; Baulier et al., 2006; Dieckmann and Heino, 2007; Mollet et al., 2007; Heino and
38 Dieckmann, 2008a, 2008b; Thériault et al., 2008; Arlinghaus et al., 2009; Okamoto et al.,
39 2009). These concerns add to those raised more broadly about the negative impact of fisheries
40 on the ecosystems in which all fish stocks are embedded (e.g., Jennings and Kaiser, 1998).
41 Concerns are exacerbated by the fact that effects of fisheries-induced evolution are building
42 up cumulatively, and by model-based results indicating that such effects will often be difficult
43 and slow to reverse (Dunlop et al., 2009a; Enberg et al., 2009).

44 Earlier theoretical studies using age-structured models have shown that increased harvest-
45 ing pressures may cause evolutionary shifts toward earlier maturation (Law and Grey, 1989;
46 Heino, 1998; Ernande et al., 2004). The corresponding selection pressures are often enhanced
47 when harvesting is positively size-selective, i.e., when larger fish are exploited more heavily
48 than smaller fish. This picture has been complemented by recent studies demonstrating that in
49 the presence of life-history trade-offs and/or predation, harvest-induced evolution may also
50 result in delayed maturation (Gårdmark et al., 2003; Gårdmark and Dieckmann 2006). These
51 newer predictions are based on specific assumptions about the trade-off between early matu-
52 ration and growth, and therefore between early maturation and subsequent fecundity. Since
53 there are several ways in which early maturation may cause fitness costs, and since the as-
54 sumptions made about the resultant trade-offs are likely to impact the evolutionary
55 predictions, further scrutiny of these dependences is warranted. As the major competing func-
56 tions in an individual's allocation of available resources are reproduction, survival, and
57 growth (e.g., Roff, 1983; Charnov and Berrigan, 1991; Arendt, 1997; Fonseca and Cabral,
58 2007), it is natural to consider that early maturation may result in reduced fecundity, reduced
59 growth, and/or increased natural mortality. In this study, we systematically explore the evolu-
60 tionary impacts of fishing under all these scenarios.

61 Also, earlier theoretical studies of fisheries-induced evolution have largely focused on
 62 size-selective fishing. This reflects the fact that many of the world's fisheries are harvested
 63 size-selectively, because of gear design, targeting incentives of fishers, or management regu-
 64 lations (e.g., Holden, 1994; Hart and Reynolds, 2002; Fromentin and Powers, 2005). Some
 65 fisheries, however, may also be selective with respect to the maturity stage of individuals, ir-
 66 respective of their size. While such an exploitation pattern is less common, it readily occurs
 67 when fisheries selectively target a stock's spawning grounds, like in the cases of Northeast
 68 Arctic cod (e.g., Garrod, 1967; Opdal, 2010) and Norwegian spring-spawning herring (e.g.,
 69 Dragesund et al., 1980; Engelhard and Heino, 2004). At first sight, such stage-specific selec-
 70 tivity may appear to be very similar to size-specific harvesting, as mature individuals tend to
 71 be large individuals and vice versa. It is therefore important to realize that the evolutionary
 72 implications of stage-specific exploitation may surprisingly differ from those of size-specific
 73 exploitation. In this study, we systematically explore the evolutionary impacts of fishing un-
 74 der both scenarios.

75 In the following sections, we investigate maturation evolution in a size-structured conti-
 76 nuous-time model of a selectively harvested population. In particular, we extend previous
 77 analyses by systematically exploring the evolutionary implications of (1) different fitness
 78 costs of early maturation, which may imply reduced fecundity, reduced growth, and/or in-
 79 creased natural mortality; and of (2) different selectivities of the harvesting regime, which
 80 may be based on size or on maturity stage.

81 **2. Model description**

82 We consider a harvested population divided into three size classes, as illustrated in Figure 1.

83 **2.1 Life-history processes**

84 Newborn individuals enter the first size class, grow into the second size class at rate r_1 , and
 85 from there grow into the third size class. With probability γ , individuals mature when enter-
 86 ing the second size class (early maturation); otherwise, they mature when entering the third
 87 size class (late maturation). Late-maturing individuals grow into the third size class at rate r_2 ,
 88 while early-maturing individuals grow into the third size class at rate \tilde{r}_2 . Late-maturing indi-
 89 viduals produce offspring at rate f_3 , while early-maturing individuals produce offspring at
 90 rate \tilde{f}_2 in the second size class and at rate \tilde{f}_3 in the third. Late-maturing individuals expe-
 91 rience mortality rates m_2 and m_3 in the second and third size class, respectively, while early-
 92 maturing individuals experience the corresponding mortality rates \tilde{m}_2 and m_3 . Natural mor-
 93 tality in the first size class is density-dependent and of logistic type, with carrying capacity

94 $1/m_1$. Harvesting is assumed to be density-independent and to occur in the second and/or
 95 third size classes, with rates of harvest mortality denoted by h_2 (individuals in the second size
 96 class that are late-maturing and thus immature), \tilde{h}_2 (individuals in the second size class that
 97 are early-maturing and thus mature), and h_3 (individuals in the third size class, which are all
 98 mature). The densities of individuals are denoted by N_1 (individuals in the first size class,
 99 which are all immature), N_2 (individuals in the second size class that are late-maturing and
 100 thus immature), \tilde{N}_2 (individuals in the second size class that are early-maturing and thus ma-
 101 ture), N_3 (late-maturing individuals in the third size class, which are all mature), and \tilde{N}_3
 102 (early-maturing individuals in the third size class, which are all mature). Quantities with a
 103 tilde always refer to the early-maturing life history. Table 1 provides an overview of all model
 104 variables and parameters.

105 2.2 Life-history dynamics

106 The dynamics of individuals in the first size class are given by

$$107 \quad \frac{dN_1}{dt} = \tilde{f}_2\tilde{N}_2 + \tilde{f}_3\tilde{N}_3 + f_3N_3 - m_1N_1^2 - r_1N_1 . \quad (1)$$

108 The first two terms on the right-hand side represent recruitment from early-maturing individ-
 109 uals, while the third term represents recruitment from late-maturing individuals. The last two
 110 terms represent density-dependent mortality in the first size class and growth into the second
 111 size class.

112 The dynamics of early- and late-maturing individuals in the second size class are given by,
 113 respectively,

$$114 \quad \frac{d\tilde{N}_2}{dt} = \gamma r_1 N_1 - \tilde{m}_2\tilde{N}_2 - \tilde{h}_2\tilde{N}_2 - \tilde{r}_2\tilde{N}_2 , \quad (2a)$$

$$115 \quad \frac{dN_2}{dt} = (1-\gamma)r_1N_1 - m_2N_2 - h_2N_2 - r_2N_2 . \quad (2b)$$

116 From left to right, the terms represent growth from the first size class, natural mortality, harv-
 117 est mortality, and growth into the third size class.

118 Finally, the dynamics of early- and late-maturing individuals in the third size class are
 119 given by, respectively,

$$120 \quad \frac{d\tilde{N}_3}{dt} = \tilde{r}_2\tilde{N}_2 - m_3\tilde{N}_3 - h_3\tilde{N}_3 , \quad (3a)$$

$$121 \quad \frac{dN_3}{dt} = r_2N_2 - m_3N_3 - h_3N_3 . \quad (3b)$$

122 From left to right, the terms represent growth from the second size class, natural mortality,
123 and harvest mortality.

124 **2.3 Life-history trade-offs**

125 To explore maturation evolution in our model, we examine adaptations in the probability γ
126 that an individual matures early. Like Gårdmark et al. (2003), we assume that earlier maturation
127 incurs life-history costs arising from energy-budget considerations. Limits in the energy
128 individuals can allocate to different life-history functions naturally result in trade-offs between
129 early maturation and reduced fecundity ($\tilde{f}_3 < f_3$), reduced growth ($\tilde{r}_2 < r_2$), and/or
130 increased natural mortality ($\tilde{m}_2 > m_2$). Based on these trade-offs and the dynamics specified
131 above, we now investigate the selection pressures harvesting imposes on the quantitative trait
132 γ .

133 **3. Evolutionary consequences of size-specific harvesting**

134 To determine the fitness differences between early- and late-maturing individuals, we consider
135 their basic reproduction ratio,

$$136 \quad R_0 = F_2 T_2 + F_3 T_3, \quad (4)$$

137 where F_2 and F_3 denote, respectively, the average fecundity rate of an individual in the
138 second and third size class, while T_2 and T_3 denote the average time individuals spend in
139 these two size classes. Early maturation increases F_2 , but the trade-offs with growth, mortality,
140 and/or fecundity will additionally affect T_2 , T_3 , and/or F_3 , making the overall effect on
141 R_0 hard to intuit. Table 2 summarizes the qualitative impacts that early maturation has on F_2 ,
142 F_3 , T_2 , and T_3 under the three types of trade-offs. To proceed, a quantitative analysis is required.
143

144 **3.1 Evolutionary invasion analysis**

145 With $R_0 = \gamma R_0^1 + (1 - \gamma) R_0^0$, where R_0^1 and R_0^0 are the basic reproduction ratios for early- and
146 late-maturing individuals, respectively, we see that early maturation is favored by selection if
147 and only if $R_0^1 > R_0^0$ (bang-bang control; Sonneborn and Van Vleck, 1965). In Appendix A,
148 we show that this inequality is equivalent to

$$149 \quad \tilde{D}_2 \tilde{f}_2 > r_2 D_2 D_3 f_3 - \tilde{r}_2 \tilde{D}_2 D_3 \tilde{f}_3, \quad (5)$$

150 where D_i denotes the average time that a late-maturing individual entering size class $i = 2, 3$
151 will remain in that size class. Likewise, \tilde{D}_2 denotes the average time that an early-maturing

152 individual entering the second size class will remain in that size class. The difference between
 153 D_i and \tilde{D}_i on the one hand, and T_i on the other, is that the former measure the average time
 154 an individual entering a size class will remain there, whereas the latter measure the average
 155 time a newborn individual will stay in size class i during the course of its life. Ineq. (5) can
 156 be interpreted as describing a trade-off between the fitness gains due to early maturation in the
 157 second size class and the fitness losses due to early maturation in the third size class that re-
 158 sult from reduced fecundity rate, reduced growth rate, and/or increased natural mortality rate.

159 The expected duration individuals spend in a size class is given by the inverse of their exit
 160 rate from that size class,

$$161 \quad D_2 = \frac{1}{m_2 + h_2 + r_2}, \quad \tilde{D}_2 = \frac{1}{\tilde{m}_2 + \tilde{h}_2 + \tilde{r}_2}, \quad \text{and} \quad D_3 = \frac{1}{m_3 + h_3}. \quad (6)$$

162 Substituting Eqs. (6) into Ineq. (5) and reorganizing shows that early maturation is favored by
 163 selection if and only if

$$164 \quad \tilde{f}_2 > \frac{1}{m_3 + h_3} \left(\frac{\tilde{m}_2 + \tilde{h}_2 + \tilde{r}_2}{m_2 + h_2 + r_2} r_2 f_3 - \tilde{r}_2 \tilde{f}_3 \right). \quad (7)$$

165 This inequality allows us to conclude that harvesting the third size class always promotes ear-
 166 ly maturation. The consequences of harvesting the second size class at a stage-unspecific rate
 167 $h_2 = \tilde{h}_2$ are less obvious and are examined below for each of the three potential costs of early
 168 maturation. It should be noted, however, that too high harvest mortality rates may cause the
 169 population to go extinct. Hence, conclusions drawn from Ineq. (7) are meaningful only for
 170 parameter values at which the population persists. A comprehensive graphical representation
 171 of possible outcomes of harvesting the second size class, also accounting for the exploitation
 172 limits at which the population goes extinct, is given in Fig. 2.

173 3.2 Trade-off between early reproduction and fecundity rate

174 Assuming that the only cost of early maturation is reduced fecundity in the third size class,
 175 $\tilde{f}_3 < f_3$, Ineq. (7) simplifies to

$$176 \quad \tilde{f}_2 > \frac{r_2(f_3 - \tilde{f}_3)}{m_3 + h_3}. \quad (8)$$

177 In this case, harvesting the second size class does not affect maturation evolution. This is be-
 178 cause an increased mortality rate in the second size class equally reduces an individual's
 179 probability of reaching the third size class and its time spent in the second size class.

180 3.3 Trade-off between early reproduction and growth rate

181 When early maturation reduces the growth rate of mature individuals, $\tilde{r}_2 < r_2$, Ineq. (7) simpli-
182 fies to

$$183 \quad \tilde{f}_2 > \frac{f_3(m_2 + h_2)(r_2 - \tilde{r}_2)}{(m_3 + h_3)(m_2 + h_2 + r_2)}. \quad (9)$$

184 In contrast to the preceding case, the mortality rates in the second size class do affect this in-
185 equality, and may therefore cause maturation evolution. Harvesting individuals in the second
186 size class causes the right-hand side of Ineq. (9) to increase, thus making early maturation less
187 advantageous.

188 3.4 Trade-off between early maturation and mortality rate

189 When early maturation increases the natural mortality rate of mature individuals in the second
190 size class, $\tilde{m}_2 > m_2$, Ineq. (7) simplifies to

$$191 \quad \tilde{f}_2 > \frac{f_3 r_2 (\tilde{m}_2 - m_2)}{(m_3 + h_3)(m_2 + h_2 + r_2)}. \quad (10)$$

192 Here, the right-hand side decreases if the harvesting mortality rate increases, so harvesting the
193 second size class makes early maturation more advantageous.

194 3.5 Multiple trade-offs associated with early maturation

195 The analysis above shows how the evolutionary effects of harvesting the second size class
196 vary with the considered trade-off. To understand what happens when the three trade-offs are
197 considered simultaneously, we denote by f_2^* the right-hand side of Ineq. (7) for $h_2 = \tilde{h}_2$, and
198 calculate the first derivative of f_2^* with respect to h_2 ,

$$199 \quad \frac{\partial f_2^*}{\partial h_2} = \frac{f_3 r_2 (m_2 - \tilde{m}_2 + r_2 - \tilde{r}_2)}{(m_3 + h_3)(m_2 + h_2 + r_2)^2}. \quad (11)$$

200 We see that the sign of this derivative depends only on $m_2 - \tilde{m}_2 + r_2 - \tilde{r}_2$: harvesting the
201 second size class makes early maturation more (less) advantageous if $m_2 - \tilde{m}_2 + r_2 - \tilde{r}_2 < (>) 0$,
202 i.e., if $\tilde{m}_2 - m_2 > (<) r_2 - \tilde{r}_2$, i.e., if the increase in mortality rate caused by early maturation is
203 larger (smaller) than the decrease in growth rate caused by early maturation.

204 3.6 Conclusion

205 We have analyzed the effects of size-specific harvesting on maturation evolution for three po-
206 tential costs of early maturation: reduced fecundity, reduced growth, and/or increased natural

207 mortality. Results are summarized in Table 3: harvesting the smallest size class has no effect
 208 on maturation evolution, harvesting the intermediate size class can favor either early maturation
 209 (when mortality costs exceed growth costs) or late maturation (when growth costs exceed
 210 mortality costs), while harvesting the largest size class always favors early maturation. As
 211 noted in Sec. 3.1, our analysis applies to the full parameter ranges in which the population
 212 remains extant. In Fig. 3, we demonstrate that each of the predicted outcomes does indeed occur.
 213

214 **4. Evolutionary consequences of stage-specific harvesting**

215 Using an analysis similar to that in the previous section, we can explore the effects of stage-
 216 specific harvesting, to examine the evolutionary consequences we expect from harvesting either
 217 mature or immature individuals. This scenario applies when fisheries selectively target a
 218 stock's spawning grounds or nursery grounds.

219 **4.1 Evolutionary invasion analysis**

220 We first analyze the case of stage-specific harvesting in which only immature individuals are
 221 harvested: $\tilde{h}_2 = h_3 = 0$ and $h_2 = h_{\text{imm}}$. From Ineq. (7), we see that early maturation is advanta-
 222 geous if and only if

$$223 \quad \tilde{f}_2 > \frac{1}{m_3} \left(\frac{\tilde{m}_2 + \tilde{r}_2}{m_2 + h_{\text{imm}} + r_2} r_2 f_3 - \tilde{r}_2 \tilde{f}_3 \right). \quad (12)$$

224 The evolutionary effects caused by the harvesting of immature individuals depend on whether
 225 the right-hand side of this inequality increases or decreases with respect to the harvest mor-
 226 tality rate h_{imm} , given that the population persists. Since the right-hand side of Ineq. (12) is a
 227 decreasing function of h_{imm} , harvesting immature individuals always promotes early maturation.
 228 This is true for any combination of costs of early maturation we may consider. The
 229 biological interpretation of this result derives from the fact that maturation in the second size
 230 class offers an effective refuge from a harvesting regime that exploits only immature individ-
 231 uals.

232 We now turn to stage-specific harvesting regimes that target only mature individuals:
 233 $h_2 = 0$ and $\tilde{h}_2 = h_3 = h_{\text{mat}}$. From Ineq. (7), we see that early maturation is then favored by se-
 234 lection if and only if

$$235 \quad \tilde{f}_2 > \frac{1}{m_3 + h_{\text{mat}}} \left(\frac{\tilde{m}_2 + h_{\text{mat}} + \tilde{r}_2}{m_2 + r_2} r_2 f_3 - \tilde{r}_2 \tilde{f}_3 \right). \quad (13)$$

236 As the evolutionary consequences of harvesting mature individuals are difficult to elucidate
 237 when multiple trade-offs are considered simultaneously, we explore these consequences for
 238 each of the three trade-offs in turn.

239 **4.2 Trade-off between early reproduction and fecundity rate**

240 When the sole cost of early maturation is a reduced fecundity rate in the third size class, the
 241 consequences of harvesting mature individuals are found by setting $\tilde{r}_2 = r_2$ and $\tilde{m}_2 = m_2$ and
 242 differentiating the right-hand side of Ineq. (13) with respect to h_{mat} . In Appendix B, we show
 243 that the sign of this derivative is positive for small positive values of $f_3 - \tilde{f}_3$, i.e., for small
 244 fecundity costs of early maturation. In that case, harvesting of mature individuals will make
 245 late maturation more advantageous. However, if the fecundity cost $f_3 - \tilde{f}_3$ of early maturation
 246 is high, harvesting mature individuals may have the opposite effect, by making early maturation
 247 more advantageous.

248 **4.3 Trade-off between early reproduction and growth rate**

249 If early maturation instead induces slower growth from the second to the third size class, we
 250 find that the right-hand side of Ineq. (13) is an increasing function of h_{mat} when

$$251 \quad \frac{\tilde{r}_2}{r_2} > 1 - \frac{m_3}{m_2} . \quad (14)$$

252 Thus, harvesting mature individuals makes late maturation more advantageous, independent
 253 of costs in terms of slower growth, if the natural mortality of late-maturing individuals is larger
 254 in the third size class than in the second. Otherwise, two disparate outcomes are possible. If
 255 the growth costs of early maturation are sufficiently small for Ineq. (14) to hold, i.e., if \tilde{r}_2 is
 256 not much smaller than r_2 , harvesting mature individuals makes late maturation more advanta-
 257 geous. For larger costs of early maturation, harvesting of mature individuals has the opposite
 258 effect, by making early maturation more advantageous.

259 **4.4 Trade-off between early maturation and mortality rate**

260 Examining Ineq. (13) shows that when early maturation increases the natural mortality rate in
 261 the second size class, harvesting of mature individuals makes late maturation more advanta-
 262 geous when

$$263 \quad \tilde{m}_2 - m_2 < m_3 , \quad (15)$$

264 i.e., when the mortality cost $\tilde{m}_2 - m_2$ is low, but will have the opposite effect when this mor-
 265 tality cost exceeds the intrinsic mortality rate in the third size class.

266 **4.5 Understanding the evolutionary outcomes**

267 The finding that harvesting mature individuals can induce not only late maturation (when
268 costs of early maturation are low), but also early maturation (when costs of early maturation
269 are high) is novel and surprising, but can be understood with the help of Fig. 1.

270 When costs of early maturation are negligible and harvesting is absent, early and late ma-
271 turing individuals have very similar life histories, which differ only in the additional offspring
272 early-maturing individuals produce in the second size class. Evidently, early maturation hence
273 is the better strategy, but its advantage may be arbitrarily small. When mature individuals are
274 harvested, this advantage is altered, since early-maturing individuals experience harvest mor-
275 tality in both the second and the third size class, whereas late-maturing individuals experience
276 harvesting mortality only in the third size class. Provided that the advantage of early matura-
277 tion is not too large in the absence of harvesting, the differential impact of harvesting mature
278 individuals will thus tip the evolutionary balance in favor of late maturation. This tendency is
279 already well known and understood.

280 The reasons why harvesting mature individuals can induce early maturation when costs of
281 early maturation are high are more subtle, and require appreciating two consequences of in-
282 tensive harvesting: firstly, such harvesting makes it increasingly unlikely that early-maturing
283 individuals reach the third size class, and secondly, it increasingly equalizes the expected du-
284 rations early-maturing individuals spend in the second size class and late-maturing individuals
285 spend in the third size class. Together, these effects imply a natural evolutionary advantage
286 for early-maturing individuals under the intensive harvesting of mature individuals, since
287 these individuals avoid the loss of time, and the resultant increase in mortality risk, that late-
288 maturing individuals experience in the second size class before they start to reproduce. Using
289 these overarching observations, we now consider each life-history trade-off in turn.

290 When the trade-off between early maturation and fecundity rate is sufficiently strong, the
291 third size class effectively acts as a reproductive sink for early-maturing individuals, exerting
292 a high direct fitness cost of early maturation. In the absence of harvesting, this promotes late
293 maturation. This fitness cost, however, becomes less and less relevant as the intensive har-
294 vesting of mature individuals increasingly prevents early-maturing individuals from reaching
295 the third size class. Because of the natural evolutionary advantage of early maturation de-
296 scribed above, such harvesting just needs to become intensive enough to tip the evolutionary
297 balance in favor of early maturation.

298 When the trade-off between early maturation and growth rate is sufficiently strong, the
299 growth of early-maturing individuals into the third size class is much impeded. If the natural

300 mortality of late-maturing individuals is smaller in the third size class than in the second
301 (Sect. 4.3), the expected duration that, in the absence of harvesting, late-maturing individuals
302 spend in the third size class always exceeds that of early-maturing individuals in the second
303 size class, which advantages late maturation. As the harvesting of mature individuals is in-
304 creased, these durations become similar, so the aforementioned advantage of late maturation
305 gradually disappears. At the same time, early-maturing individuals become unlikely to reach
306 the third size class, whether they grow well or not, so the relative importance of the direct fit-
307 ness cost of early maturation also gradually disappears. What remains is the natural
308 evolutionary advantage of early maturation, which thus inevitably prevails once harvesting is
309 intensive enough.

310 Finally, when the trade-off between early maturation and mortality rate is sufficiently
311 strong, early-maturing individuals experience a higher natural mortality in the second size
312 class. In the absence of harvesting, this promotes late maturation. As the harvesting of mature
313 individuals is intensified, however, this direct fitness cost of early maturation is increasingly
314 overshadowed by fishing mortality. Consequently, when such harvesting is intensive enough,
315 the natural evolutionary advantage of early maturation will dominate the outcome.

316 For all three life-history trade-offs, the high direct fitness costs of early maturation, which
317 favor late maturation in the absence of harvesting, thus gradually vanish as mature individuals
318 are harvested intensively, uncovering the natural evolutionary advantage early maturation
319 confers under such conditions.

320 **4.6 Conclusion**

321 We have analyzed the effects of stage-specific harvesting on maturation evolution for three
322 potential costs of early maturation: reduced fecundity, reduced growth, and/or increased natu-
323 ral mortality. Results are summarized in Table 3. Harvesting immature individuals always
324 favors early maturation. Harvesting mature individuals favors late maturation when the costs
325 of early maturation are low. When natural mortality in the largest size class exceeds that in the
326 intermediate size class, this conclusion remains true even when the growth costs of early ma-
327 turation are arbitrarily high. For all other cases, high costs of early maturation can reverse the
328 evolutionary consequence of harvesting mature individuals, so that such harvesting then
329 makes early maturation more advantageous. In Fig. 4, we demonstrate that each of the pre-
330 dicted outcomes does indeed occur.

331 **5. Discussion**

332 Here we have analyzed harvest-induced maturation evolution under different costs of early
333 maturation and for harvest regimes with different selectivities. In particular, we have ex-
334 amined costs of early maturation that imply reduced fecundity, reduced growth, and/or
335 increased natural mortality, while considering harvest regimes that are selective for either size
336 or maturity stage. Our results provide a first systematic overview of how the evolutionary ef-
337 fects of harvesting vary with the trade-offs associated with early maturation and with the
338 selectivities of harvesting regimes. The results of our investigation are summarized in Table 3,
339 and paraphrased in Secs. 3.6 and 4.5.

340 Life-history traits are often coupled through trade-offs (e.g., Charnov and Berrigan, 1991;
341 Stearns, 1992). In this study we have therefore considered trade-offs between size at matura-
342 tion and three major life-history characteristics: fecundity, growth, and mortality. These trade-
343 offs can affect maturation evolution by altering the underlying selection pressures. The impor-
344 tance of considering multiple trade-offs when studying harvest-induced maturation evolution
345 is demonstrated by our results: selection pressures on size at maturation caused by size- or
346 stage-specific harvesting vary, often qualitatively, with the considered life-history trade-offs.

347 Early maturation becomes advantageous when the benefits of reproducing early exceed
348 the total costs of early reproduction. We find that when the cost of early maturation reduces
349 fecundity in the largest size class, the mortality rate in the intermediate size class has no bear-
350 ing on whether early or late maturation is advantageous. At first sight, this finding contrasts
351 with earlier results obtained by Gårdmark et al. (2003). However, this difference between the
352 continuous-time size-structured model studied here and the discrete-time age-structured mod-
353 el studied by Gårdmark et al. (2003) is unsurprising, since in our model a change in the
354 mortality of the intermediate size class does not only affect the probability of reaching the
355 largest size class, but also the time spent in the intermediate size class. This is not the case in
356 the model by Gårdmark et al. (2003), where the time spent in the intermediate age class is
357 fixed.

358 Harvest regimes are often selective in the sense that the mortality caused by fishing may
359 depend on size, age, and/or maturity stage (e.g., Ajiad et al., 1999; Law, 2000). While age-
360 specific harvesting is rare, size- and stage-specific harvesting are common. The results of our
361 study underscore that the latter harvest selectivities can qualitatively change the outcomes of
362 maturation evolution: harvesting intermediately sized or mature individuals can favor either
363 early or late maturation (depending on the costs of early maturation), whereas harvesting large
364 or immature individuals always favors early maturation.

365 Previous studies have already shed some light on maturation evolution under harvest re-
366 gimes that select for size or maturity stage. A study by Ernande et al. (2004) predicted that the
367 harvesting of mature individuals induces maturation at an older age and larger size, whereas
368 the harvesting of immature individuals induces maturation at a younger age and smaller size.
369 Their work generalized earlier findings by Law and Grey (1989) and Heino (1998), which
370 were obtained for directly evolving age or size at maturation, respectively, to ages and sizes at
371 maturation that plastically varied with juvenile growth conditions. Our results differ from
372 these findings by showing that harvesting of mature individuals may either increase or de-
373 crease the size at maturation that is favored by selection. Our results confirm findings by
374 Gårdmark et al. (2006), who showed that evolutionary outcomes in size at maturation can
375 both increase and decrease as a result of size-specific harvesting. Our results are novel by
376 showing how the alternative fitness costs of early maturation determine the evolutionary con-
377 sequences of harvesting.

378 For harvesting to decrease the size at maturation, the direct fitness cost of early maturation
379 must be large. As an example, when this cost is expressed in terms of higher natural mortality,
380 the harvesting of mature individuals may cause early maturation only if the additional mortali-
381 ty rate exceeds the natural mortality rate of the third size class. As another example, when the
382 cost of early maturation is expressed in terms of lower growth, and natural mortality in the
383 third size class is 10 percent lower than in the second, the harvesting of mature individuals
384 may cause early maturation only if the early-maturing individuals grow 10 times slower than
385 the late-maturing individuals. As a final example, when the cost of early maturation is ex-
386 pressed in terms of lower fecundity in the third size class, and the intrinsic growth and
387 mortality rates are all equal, the fecundity must be reduced by half before harvesting mature
388 individuals may cause early maturation.

389 With the number of empirical studies indicative of harvest-induced evolution in matura-
390 tion schedules of commercially exploited marine fish stocks mounting rapidly (e.g., Grift et
391 al., 2003, 2007; Olsen et al., 2004, 2005; Barot et al., 2005; Baulier et al., 2006; Mollet et al.,
392 2007; Okamoto et al., 2009), it is becoming increasingly important to interpret observed
393 trends in terms of sufficiently realistic eco-evolutionary models. Since, as a matter of prin-
394 ciple, it will never be possible to prove fisheries-induced evolution as the unequivocal cause
395 of maturation trends (Dieckmann and Heino, 2007), models are key to assessing whether the
396 observed trends comply with those predicted by life-history theory: the closer the match, the
397 more an interpretation of observed trends in terms of fisheries-induced evolution is streng-
398 thened.

399 In response to this need, various eco-evolutionary modeling approaches have been devised
400 and analyzed. The pioneering work by Law and Grey (1989) addressed harvest-induced matu-
401 ration evolution in terms of simple age-structured population models (see also Rowell, 1993;
402 Rijnsdorp, 1993b; Heino, 1998). Since then, several studies have extended the modeling of
403 harvest-induced evolution to, e.g., natural predation (Gårdmark et al., 2003), phenotypically
404 plastic growth and maturation (Ernande et al., 2004), the effects of marine reserves (Baskett et
405 al., 2005; Dunlop et al., 2009b; Mithé et al., 2010), continuous size structure (Gårdmark and
406 Dieckmann, 2006), density-dependent growth and genetic variation in multiple life-history
407 traits (Dunlop et al., 2009a), density-dependent harvesting behavior (Arlinghaus et al., 2009),
408 processes of stock recovery (Enberg et al., 2009), and explicit resource dynamics (Okamoto et
409 al., 2009). The present study adds to this portfolio of modeling approaches by elucidating the
410 effects of life-history trade-offs on harvest-induced maturation evolution.

411 A strong feature of the analysis presented here is that all results have been derived analyti-
412 cally, rather than through numerical explorations. Naturally, this benefit comes at the cost of a
413 relatively simple model structure, defined by three size classes. As a particularly promising
414 direction for future research, it will therefore be desirable to generalize our analysis to popula-
415 tions with continuous size structure, and if possible, with phenotypically plastic growth and
416 maturation. Until then, our analysis can best be applied to natural populations by recognizing
417 that our model's intermediate size class is to be defined as spanning the range of sizes over
418 which maturation can naturally occur.

419 Predictions of our study can readily be judged against empirical observations of matura-
420 tion evolution. Here we mention just a few examples. Positively size-selective fishing is
421 common among stocks that are harvested by trawl fisheries. These gears generally have catch
422 selectivity curves that increase with fish length (e.g., Millar, 1992). Examples of such stocks
423 include North Sea sole and North Sea plaice, where both mature and immature fish experience
424 positively size-selective harvest mortality rates. Our results summarized in Table 3, for the
425 "Harvesting of size class 3", are compatible with the observed trends towards maturation at
426 smaller size (Rijnsdorp, 1993; Grift et al., 2003, 2007; Mollet et al., 2007) observed for these
427 and many other stocks.

428 Stage-specific fishing is common among stocks that undergo spawning migrations. Exam-
429 ples of such stocks include Northeast Arctic cod and Norwegian spring-spawning herring,
430 where a strong spatio-temporal segregation of mature and immature fish enables targeted fi-
431 sheries. Our results summarized in Table 3, for the "Harvesting of mature individuals", are
432 compatible with the maturation sizes observed for Northeast Arctic cod until about the middle
433 of the 20th century, recognizing that these sizes were unusually large compared with all other

434 stocks of Atlantic cod, that costs of early maturation are thought to be relatively low in this
435 stock, and that the historical fishing regime had predominantly targeted mature individuals
436 (Law and Grey, 1989; Jørgensen, 1990). Furthermore, our results summarized in Table 3, for
437 the “Harvesting of immature individuals”, are compatible with the maturation sizes observed
438 for Northeast Arctic cod since about the middle of the 20th century, recognizing that harvest
439 mortality rates of immature Northeast Arctic cod in the Barents Sea has increased by a factor
440 of approximately 5-7 from 1920 to 1960. Finally, our results summarized in Table 3, for the
441 “Harvesting of mature individuals”, are compatible with the maturation sizes observed for
442 Norwegian spring-spawning herring during the 20th century. For this stock, a marked decrease
443 in growth after maturation indicates that the trade-offs between early maturation and growth,
444 and thus also between early maturation and future fecundity, are strong (Engelhard et al.,
445 2003). In accordance with our results, the evolutionary changes in size at maturation caused
446 by intense harvesting on the spawning grounds of Norwegian spring-spawning herring have
447 been found to be very small (Engelhard and Heino, 2004).

448 In conclusion, we have systematically explored how different aspects of individual life-
449 history characteristics and harvesting regimes affect the relative evolutionary advantage of
450 early maturation. To keep the analysis tractable, the ecological environment – consisting of
451 prey, competitors, and predators – has not been included in our model, even though it may
452 have confounding effects on maturation evolution (e.g., Gårdmark et al., 2003). Despite this
453 simplification, we hope that the insights on the evolutionary consequence of harvesting under
454 different life-history trade-offs obtained in this study make a helpful contribution to the rapid-
455 ly growing body of knowledge on fisheries-induced adaptive changes required for rational
456 fisheries management.

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605 **Appendix A: General invasion condition derived from basic reproduction ratio**

606 An individual's basic reproduction ratio R_0 equals its total lifetime reproductive output. For
 607 our model, this can be expressed as $R_0 = F_2T_2 + F_3T_3$, where T_2 and T_3 are the average times
 608 an individual will spend in the two larger size classes, and F_2 and F_3 are the average fecundi-
 609 ty rates in these size classes.

610 Accounting for the fact that an individual may or may not mature early, we obtain

$$611 \quad T_2 = \gamma P_2 \tilde{D}_2 + (1 - \gamma) P_2 D_2, \quad (\text{A.1})$$

612 where γ is the individual's probability to mature early (i.e., in the second size class), P_2 is its
 613 probability of surviving from entering the first size class until entering the second size class,
 614 while \tilde{D}_2 and D_2 are the average durations, respectively, that an early- and late-maturing in-
 615 dividual entering the second size class will remain there. An individual's average fecundity
 616 rate F_2 in the second size class equals the average total number of offspring it has while stay-
 617 ing in that size class, divided by the average time T_2 it spends in that size class,

$$618 \quad F_2 = \frac{\gamma P_2 \tilde{D}_2 f_2}{\gamma P_2 \tilde{D}_2 + (1 - \gamma) P_2 D_2}. \quad (\text{A.2})$$

619 Analogously, the average time an individual spends in the third size class is

$$620 \quad T_3 = \gamma P_2 \tilde{P}_3 D_3 + (1 - \gamma) P_2 P_3 D_3, \quad (\text{A.3})$$

621 where \tilde{P}_3 and P_3 , respectively, are the probabilities with which an early- and late-maturing
 622 individual entering the second size class will survive until entering the third size class. The
 623 average fecundity in the third size class is then given by

$$624 \quad F_3 = \frac{\gamma \tilde{P}_3 D_3 \tilde{f}_3 + (1 - \gamma) P_3 D_3 f_3}{\gamma \tilde{P}_3 D_3 + (1 - \gamma) P_3 D_3}. \quad (\text{A.4})$$

625 For R_0 , we thus obtain

$$626 \quad R_0 = F_2 T_2 + F_3 T_3 = \gamma (P_2 D_2 \tilde{f}_2 + P_2 \tilde{P}_3 D_3 \tilde{f}_3) + (1 - \gamma) P_2 P_3 D_3 f_3. \quad (\text{A.5})$$

627 This has to equal $R_0 = \gamma R_0^1 + (1 - \gamma) R_0^0$, where R_0^1 and R_0^0 , respectively, are the basic repro-
 628 duction ratios for early- and late-maturing individuals. Selection favors early maturation
 629 ($\gamma = 1$) over late maturation ($\gamma = 0$) if and only if $R_0^1 > R_0^0$. We can identify R_0^1 and R_0^0 from
 630 Eq. (A.5) to get

$$631 \quad P_2 \tilde{D}_2 f_2 + P_2 D_3 \tilde{P}_3 \tilde{f}_3 > P_2 P_3 D_3 f_3. \quad (\text{A.6})$$

632 Since P_2 is positive, we can rewrite Ineq. (A.6) as

$$633 \quad \tilde{D}_2 f_2 + D_3 \tilde{P}_3 \tilde{f}_3 > P_3 D_3 f_3 . \quad (\text{A.7})$$

634 The probability P_3 of an early-maturing individual entering the second size class to survive
 635 until entering the third size class is $r_2 D_2$. Similarly, the probability \tilde{P}_3 of a late-maturing indi-
 636 vidual entering the second size class to survive until entering the third size class is $\tilde{r}_2 \tilde{D}_2$. In
 637 conclusion, we therefore find that early maturation is favored by selection if

$$638 \quad \tilde{D}_2 f_2 > r_2 D_2 D_3 f_3 - \tilde{r}_2 \tilde{D}_2 D_3 \tilde{f}_3 . \quad (\text{A.8})$$

639 **Appendix B: Specific invasion conditions for harvesting mature individuals**

640 We can determine whether the harvesting of mature individuals makes early maturation more
 641 or less evolutionarily advantageous by studying how a change in the harvest mortality rate
 642 h_{mat} affects the right-hand side of Ineq. (13).

643 First, we assume that the only trade-off associated with early reproduction is a reduced fe-
 644 cundity in the third size class. Denoting by f_2^* the right-hand side of Ineq. (13) for $\tilde{r}_2 = r_2$ and
 645 $\tilde{m}_2 = m_2$, and differentiating f_2^* with respect to h_{mat} , we obtain

$$646 \quad \frac{\partial f_2^*}{\partial h_{\text{mat}}} = \frac{r_2 (\tilde{f}_3 (m_2 + r_2) - f_3 (m_2 - m_3 + r_2))}{(h_{\text{mat}} + m_3)^2 (m_2 + r_2)} . \quad (\text{B.1})$$

647 The sign of this derivative depends only on the last factor in the numerator, and therefore is
 648 positive if and only if

$$649 \quad f_3 - \tilde{f}_3 < \frac{f_3 m_3}{m_2 + r_2} . \quad (\text{B.2})$$

650 Consequently, f_2^* is an increasing function of h_{mat} when $f_3 - \tilde{f}_3$ is small, i.e., harvesting ma-
 651 ture individuals promotes late maturation when the fecundity costs of early maturation are
 652 low.

653 Second, we instead assume that the only trade-off associated with early maturation is a
 654 higher natural mortality in the second size class. Denoting by f_2^* the right-hand side of Ineq.
 655 (13) for $\tilde{f}_3 = f_3$ and $\tilde{r}_2 = r_2$, and differentiating f_2^* with respect to h_{mat} , we obtain

$$656 \quad \frac{\partial f_2^*}{\partial h_{\text{mat}}} = \frac{r_2 f_3 (m_2 - \tilde{m}_2 + m_3)}{(h_{\text{mat}} + m_3)^2 (m_2 + r_2)} . \quad (\text{B.4})$$

657 The last factor in the numerator shows that this derivative is positive if and only if

$$658 \quad \tilde{m}_2 - m_2 < m_3 , \quad (\text{B.5})$$

659 Consequently, f_2^* is an increasing function of h_{mat} when $\tilde{m}_2 - m_2$ is small, i.e., harvesting
 660 mature individuals promotes late maturation when the mortality costs of early maturation are
 661 low.

662 Third, we instead assume that the only trade-off associated with early maturation is a lower
 663 growth rate from the second to the third size class. Denoting by f_2^* the right-hand side of In-
 664 eq. (13) for $\tilde{f}_3 = f_3$ and $\tilde{m}_2 = m_2$, and differentiating f_2^* with respect to h_{mat} , we obtain

$$665 \quad \frac{\partial f_2^*}{\partial h_{\text{mat}}} = \frac{f_3(m_3 r_2 + m_2(\tilde{r}_2 - r_2))}{(h_{\text{mat}} + m_3)^2(m_2 + r_2)}. \quad (\text{B.6})$$

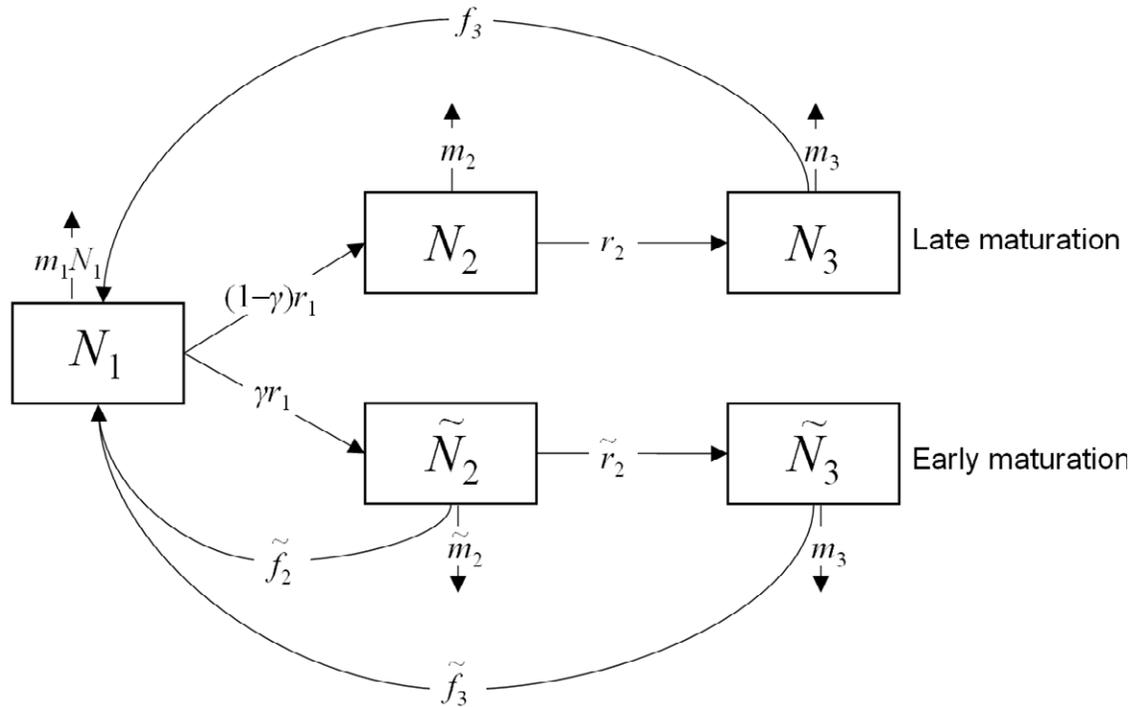
666 The last factor in the numerator shows that this derivative is positive if and only if

$$667 \quad \frac{\tilde{r}_2}{r_2} > 1 - \frac{m_3}{m_2}. \quad (\text{B.7})$$

668 For $m_3 < m_2$, f_2^* therefore is an increasing function of h_{mat} when \tilde{r}_2 / r_2 is sufficiently close to
 669 1, i.e., harvesting mature individuals promotes late maturation when the growth costs of early
 670 maturation are low. For $m_3 > m_2$, i.e., when the natural mortality rate in the third size class
 671 exceeds that in the second size class, Ineq. (B.7) holds independent of these growth costs. In
 672 that case, f_2^* always is an increasing function of h_{mat} , so that harvesting mature individuals
 673 always promotes late maturation.

674 **Appendix C: Parameter values for numerical examples**

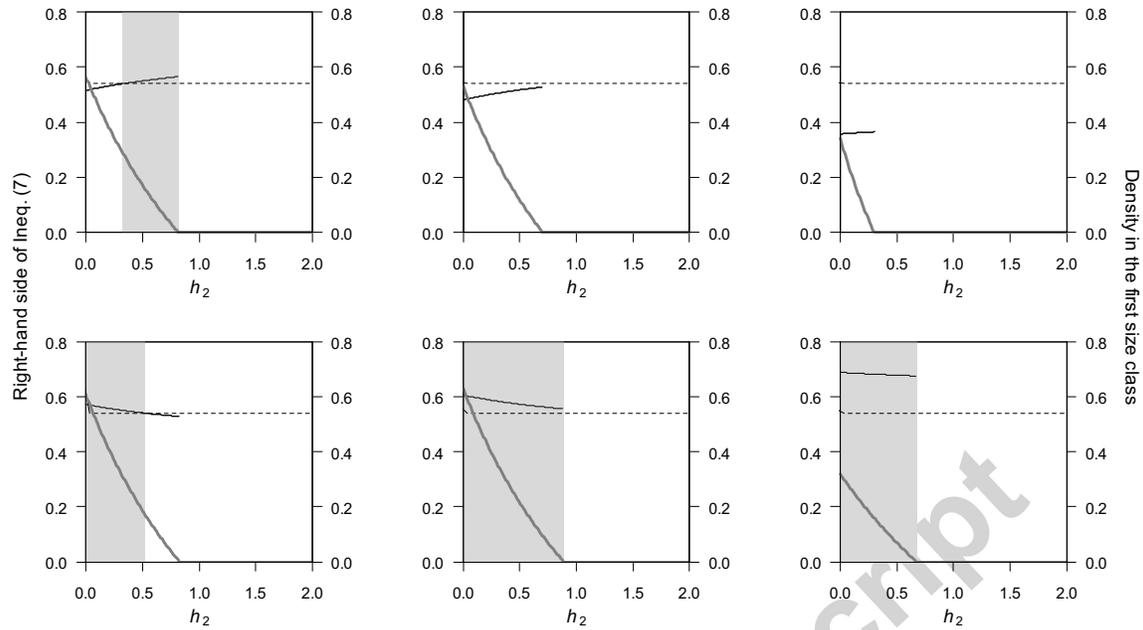
675 The analyses presented in Secs. 3 and 4 apply to the full parameter ranges for which the popu-
 676 lation persists, as illustrated in Fig. 2. In Figs. 3 and 4 we show that all predicted outcomes
 677 occur. To facilitate replication of these results, we provide in Table C1 the specific paramete-
 678 rizations that were used to produce each of the panels in Figs. 2-4.

679 **Figures and captions**

680

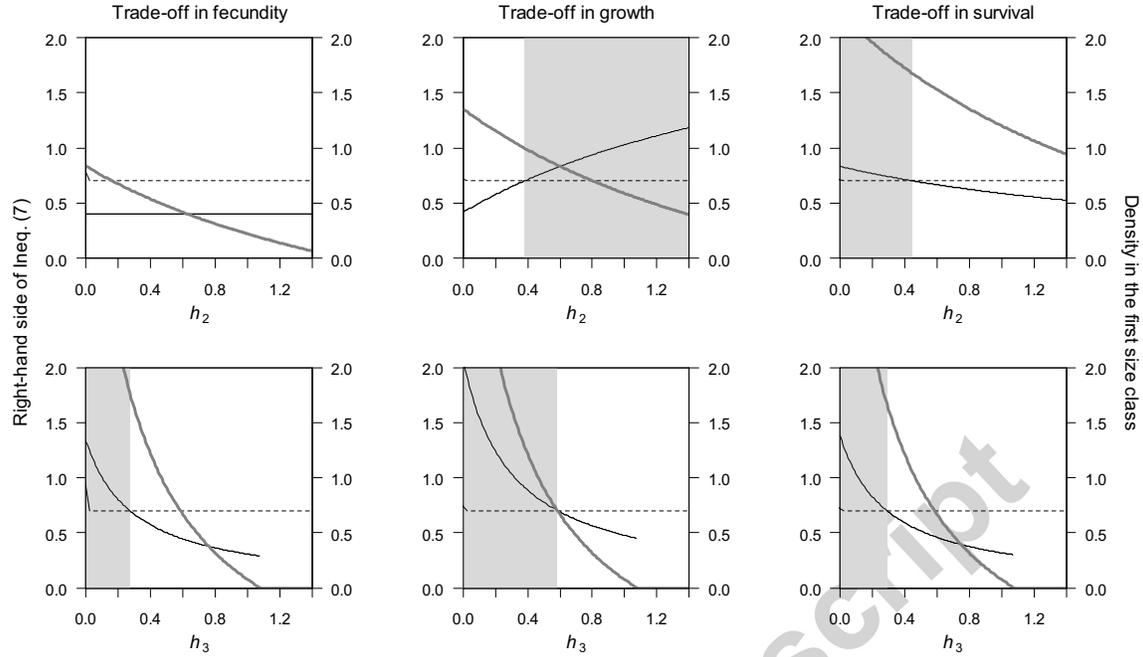
681 **Figure 1.** Schematic illustration of the size-structured continuous-time life-history model ana-
 682 lyzed in this study. The harvested population is partitioned into small individuals (first size
 683 class, with density N_1), intermediately sized individuals (second size class, with densities N_2
 684 and \tilde{N}_2), and large individuals (third size class, with densities N_3 and \tilde{N}_3). Individuals can
 685 mature early (with probability γ , bottom row) or late (with probability $1-\gamma$, top row). Quan-
 686 tities with a tilde refer to the early-maturing life history. The probability γ of early
 687 maturation is evolving. The parameters r_1 , r_2 , and \tilde{r}_2 are growth rates; \tilde{f}_2 , f_3 , and \tilde{f}_3 are fe-
 688 cundity rates; $1/m_1$ is the carrying capacity of the first size class; m_2 , \tilde{m}_2 , and m_3 are natural
 689 mortality rates; and h_2 , \tilde{h}_2 , and h_3 are harvest mortality rates.

690



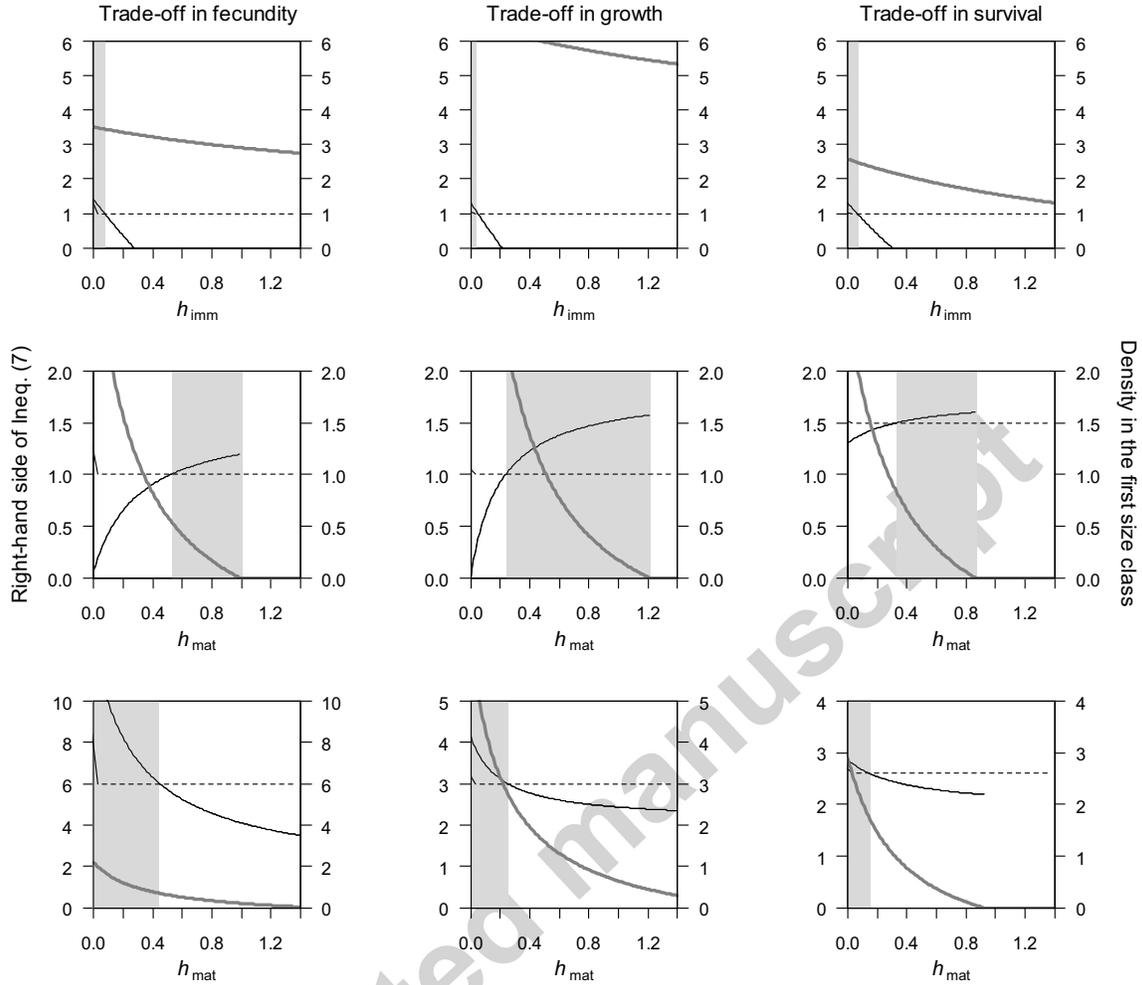
691 **Figure 2.** Numerical illustration of the possible evolutionary consequences of harvesting the
 692 second size class (increasing h_2). Harvesting the second size class can make maturation in
 693 either the second or the third size class advantageous. The population density N_1 of the first
 694 size class (thick gray line, right vertical axis) decreases with increased harvesting rate h_2 . If
 695 harvesting rates are too high for the population to persist, model predictions are not meaning-
 696 ful. The right-hand side of Ineq. (7) (thin black line, left vertical axis) can either increase with
 697 h_2 (top panels) or decrease with h_2 (lower panels), depending on model parameters. When
 698 the thin black line is below f_2 , marked here with a dashed horizontal line, Ineq. (7) is ful-
 699 filled and selection promotes early maturation. If instead the thin black line is above f_2 , Ineq.
 700 (7) is not fulfilled and selection promotes late maturation (grey areas). As the harvesting rate
 701 is increased, there may be a switch in optimal maturation size (left panels). Alternatively, the
 702 switch in optimal maturation is predicted by the model at harvesting rates for which the popu-
 703 lation is no longer viable (central panels). Finally, model parameters can be chosen such that
 704 the switching point is never reached, independent of the harvesting rate (right panels). Para-
 705 meter values are provided in Table C1 of Appendix C.

706



707 **Figure 3.** Numerical illustration showing that all predicted outcomes of size-selective harvest-
 708 ing (increasing h_2 or h_3) are possible. Figure elements are as in Fig. 2. For a trade-off
 709 between early maturation and fecundity rate, harvesting the second size class does not affect
 710 maturation in either the second or the third size class (top left panel). For a trade-off between
 711 early maturation and growth rate, harvesting the second size class promotes late maturation
 712 (top center panel). Finally, for a trade-off between early maturation and mortality rate, har-
 713 vesting promotes early maturation (top right panel). Harvesting the third size class always
 714 promotes early maturation (bottom panels). Parameter values are provided in Table C1 of Ap-
 715 pendix C.

716



717 **Figure 4.** Numerical illustration showing that all analytically predicted outcomes of stage-
 718 selective harvesting (increasing h_{imm} or h_{mat}) are possible. Figure elements are as in Fig. 2.
 719 Harvesting immature individuals always promotes early maturation (top panels). For a trade-
 720 off between early maturation and fecundity rate, harvesting mature individuals promotes late
 721 maturation when the reduction $f_3 - \tilde{f}_3$ in fecundity rate is small (middle left panel), and early
 722 maturation when $f_3 - \tilde{f}_3$ is large (bottom left panel). For a trade-off between early maturation
 723 and growth rate, harvesting mature individuals always promotes late maturation if the natural
 724 mortality in the third size class is larger than the natural mortality in the second size class (not
 725 shown). Otherwise, for all three life-history tradeoffs, harvesting mature individuals promotes
 726 late maturation when the costs of early maturation are low (middle panels) and early maturation
 727 when the costs of early maturation are high (lower panels). Parameter values are provided
 728 in Table C1 of Appendix C.

729 **Tables and captions**730 **Table 1.** Overview of model variables, parameters, and derived quantities.

Notation	Description
<i>Variables</i>	
N_1	Density of individuals in size class 1
N_i	Density of late-maturing individuals in size classes $i = 2, 3$
\tilde{N}_i	Density of early-maturing individuals in size classes $i = 2, 3$
<i>Parameters</i>	
γ	Probability of early maturation
\tilde{f}_2	Fecundity rate of early-maturing individuals in size class 2
f_3	Fecundity rate of late-maturing individuals in size class 3
\tilde{f}_3	Fecundity rate of early-maturing individuals in size class 3
m_2	Natural mortality rate of late-maturing individuals in size class 2
\tilde{m}_2	Natural mortality rate of early-maturing individuals in size class 2
m_3	Natural mortality rate of individuals in size class 3
h_i	Harvest mortality rate of late-maturing individuals in size classes $i = 2, 3$
\tilde{h}_2	Harvest mortality rate of early-maturing individuals in size class 2
h_{imm}	Harvest mortality rate of immature individuals
h_{mat}	Harvest mortality rate of mature individuals
r_1	Growth rate of individuals from size class 1 to size class 2
r_2	Growth rate of late-maturing individuals from size class 2 to size class 3
\tilde{r}_2	Growth rate of early-maturing individuals from size class 2 to size class 3
<i>Derived quantities</i>	
F_2	Average fecundity rate of individuals in size class 2
F_3	Average fecundity rate of individuals in size class 3
T_2	Average time spent by individuals in size class 2
T_3	Average time spent by individuals in size class 3
P_2	Survival probability from entering size class 1 until entering size class 2
P_3	Survival probability of late-maturing individuals from entering size class 2 until entering size class 3
\tilde{P}_3	Survival probability of early-maturing individuals from entering size class 2 until entering size class 3

D_2	Average duration of stay of late-maturing individuals entering size class 2
\tilde{D}_2	Average duration of stay of early-maturing individuals entering size class 2
D_3	Average duration of stay of individuals entering size class 3
f_2^*	Threshold for f_2 above which selection favors early maturation

731 **Table 2.** Qualitative effects of early maturation on the fecundity and average time spent in the
 732 second and third size classes, for the three different life-history trade-offs.

Trade-off of early maturation with	Effect on size class 2	Effect on size class 3
Fecundity	$F_2 \uparrow$	$F_3 \downarrow$
Growth	$F_2 \uparrow T_2 \uparrow$	$T_3 \downarrow$
Survival	$F_2 \uparrow T_2 \downarrow$	$T_3 \downarrow$

733 **Table 3.** Evolutionary effects of increased harvest mortality rate. \downarrow indicates that harvesting
 734 promotes early maturation, 0 indicates no effect, and \uparrow indicates that late maturation is pro-
 735 moted. \downarrow/\uparrow indicates that harvesting promotes early maturation when the costs of early
 736 maturation are low, while late maturation is promoted when the costs of early maturation are
 737 high.

Harvesting of	Trade-off of early maturation with		
	Fecundity	Growth	Survival
Size class 1	0	0	0
Size class 2	0	\uparrow	\downarrow
Size class 3	\downarrow	\downarrow	\downarrow
Immature individuals	\downarrow	\downarrow	\downarrow
Mature individuals	\uparrow/\downarrow	\uparrow/\downarrow or \uparrow^*	\uparrow/\downarrow

738 * When natural mortality in size class 2 exceeds that in size class 3, harvesting of mature indi-
 739 viduals promotes late maturation independent of the growth costs of early maturation.

740

741 **Table C1.** Parameter values for Figs. 2-4. Values that change within figures are shown in italics.
 742 ics. The left edges of all panels correspond to an unexploited situation: accordingly, harvest
 743 rates that are not varied in the panels are set to zero. Notice, however, that the results remain
 744 invariant if part of the natural mortality is redistributed to constant harvesting mortality.

		Parameter								
Panel		m_1	m_2	\tilde{m}_2	m_3	r_2	\tilde{r}_2	\tilde{f}_2	f_3	\tilde{f}_3
Figure 2										
Top left		0.8	<i>0.31</i>	<i>0.40</i>	1.20	<i>1.50</i>	<i>1.30</i>	0.54	2.1	1.80
Top centre		0.8	<i>0.31</i>	<i>0.40</i>	1.20	<i>1.35</i>	<i>1.15</i>	0.54	2.1	1.80
Top right		0.8	<i>0.30</i>	<i>0.40</i>	1.20	<i>0.80</i>	<i>0.67</i>	0.54	2.1	1.80
Bottom left		0.8	<i>0.26</i>	<i>0.40</i>	1.20	<i>1.45</i>	<i>1.40</i>	0.54	2.1	1.80
Bottom centre		0.8	<i>0.25</i>	<i>0.40</i>	1.20	<i>1.52</i>	<i>1.47</i>	0.54	2.1	1.80
Bottom right		0.8	<i>0.75</i>	<i>0.90</i>	1.20	<i>1.90</i>	<i>1.80</i>	0.54	2.1	1.80
Figure 3										
Top left		0.8	<i>0.4</i>	<i>0.70</i>	<i>1.00</i>	1.00	1.00	0.70	2.00	1.80
Top centre		0.8	<i>0.4</i>	<i>0.70</i>	<i>0.80</i>	1.00	1.00	0.70	2.00	1.80
Top right		0.8	<i>0.4</i>	<i>0.70</i>	<i>0.60</i>	1.00	1.00	0.70	2.00	1.80
Bottom left		0.8	<i>0.9</i>	<i>1.20</i>	<i>0.30</i>	1.00	1.00	0.70	2.00	1.80
Bottom centre		0.8	<i>0.9</i>	<i>1.20</i>	<i>0.30</i>	1.00	1.00	0.70	2.00	1.80
Bottom right		0.8	<i>0.9</i>	<i>1.20</i>	<i>0.30</i>	1.00	1.00	0.70	2.00	1.80
Figure 4										
Top left		1.3	<i>0.60</i>	<i>0.60</i>	<i>0.60</i>	2.00	2.00	<i>1.00</i>	2.20	2.00
Top centre		1.3	<i>0.40</i>	<i>0.40</i>	<i>0.20</i>	2.60	<i>1.70</i>	<i>1.00</i>	2.20	2.20
Top right		1.3	<i>0.30</i>	<i>0.60</i>	<i>0.20</i>	2.00	2.00	<i>1.00</i>	2.00	2.00
Middle left		1.3	<i>0.60</i>	<i>0.60</i>	<i>0.30</i>	2.00	2.00	<i>1.00</i>	2.20	2.00
Middle centre		1.3	<i>0.40</i>	<i>0.40</i>	<i>0.20</i>	2.00	<i>1.99</i>	<i>1.00</i>	2.20	2.20
Middle right		1.3	<i>0.30</i>	<i>0.60</i>	<i>0.40</i>	2.00	2.00	<i>1.50</i>	2.00	2.00
Bottom left		1.3	<i>0.60</i>	<i>0.60</i>	<i>0.30</i>	2.00	2.00	<i>6.00</i>	2.00	<i>0.10</i>
Bottom centre		1.3	<i>0.40</i>	<i>0.40</i>	<i>0.20</i>	8.00	<i>0.10</i>	<i>3.00</i>	2.20	2.20
Bottom right		1.3	<i>0.10</i>	<i>0.70</i>	<i>0.40</i>	2.00	2.00	<i>2.60</i>	2.00	2.00

745