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# Harvest-induced maturation evolution under different life-history trade-offs and harvesting regimes

J.J. Poos<sup>a,b,\*</sup>, Å. Brännström<sup>a,c</sup>, U. Dieckmann<sup>a</sup>

<sup>a</sup> Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361, Laxenburg, Austria

<sup>b</sup> Wageningen IMARES, Institute for Marine Resources and Ecosystem Studies, PO Box 68, 1970 AB IJmuiden, The Netherlands

<sup>c</sup> Department of Mathematics and Mathematical Statistics, Umeå University, SE-90187, Umeå, Sweden

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## ABSTRACT

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

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## 1. Introduction

Concerns over evolutionary consequences of harvesting are mounting, as both theoretical and empirical studies have demonstrated the potential for rapid harvest-induced evolution (e.g., Law, 2000; Conover and Munch, 2002; Heino and Godø, 2002; Ashley et al., 2003; Coltman et al., 2003; Jørgensen et al., 2007; Dieckmann et al., 2009). Life-history theory predicts that increased mortality devalues life-history processes occurring later in life, relative to those occurring earlier (e.g., Law, 1979; Stearns, 1992; Ernande et al., 2004). Therefore, systematic reductions in age and size at maturation observed for stocks exposed to heavy fishing (e.g., Jørgensen, 1990; Rijnsdorp, 1993a; Trippel, 1995) are suggestive of fisheries-induced evolution (e.g., Heino et al., 2002; Grift et al., 2003, 2007; Barot et al., 2004, 2005; Olsen et al., 2004, 2005; Baulier et al., 2006; Dieckmann and Heino, 2007; Mollet et al., 2007; Heino and Dieckmann, 2008a, 2008b; Thériault et al., 2008; Arlinghaus et al., 2009; Okamoto et al., 2009). These concerns add to those raised more broadly about the negative

impact of fisheries on the ecosystems in which all fish stocks are embedded (e.g., Jennings and Kaiser, 1998). Concerns are exacerbated by the fact that effects of fisheries-induced evolution are building up cumulatively, and by model-based results indicating that such effects will often be difficult and slow to reverse (Dunlop et al., 2009a; Enberg et al., 2009).

Earlier theoretical studies using age-structured models have shown that increased harvesting pressures may cause evolutionary shifts toward earlier maturation (Law and Grey, 1989; Heino, 1998; Ernande et al., 2004). The corresponding selection pressures are often enhanced when harvesting is positively size-selective, i.e., when larger fish are exploited more heavily than smaller fish. This picture has been complemented by recent studies demonstrating that in the presence of life-history trade-offs and/or predation, harvest-induced evolution may also result in delayed maturation (Gårdmark et al., 2003; Gårdmark and Dieckmann, 2006). These newer predictions are based on specific assumptions about the trade-off between early maturation and growth, and therefore between early maturation and subsequent fecundity. Since there are several ways in which early maturation may cause fitness costs, and since the assumptions made about the resultant trade-offs are likely to impact the evolutionary predictions, further scrutiny of these dependences is warranted. As the major competing functions in an individual's allocation of available resources are reproduction,

\* Corresponding author at: Wageningen IMARES, Institute for Marine Resources and Ecosystem Studies, PO Box 68, 1970 AB IJmuiden, The Netherlands. Tel.: +31317487189.

E-mail address: [janjaap.poos@wur.nl](mailto:janjaap.poos@wur.nl) (J.J. Poos).

survival, and growth (e.g., Roff, 1983; Charnov and Berrigan, 1991; Arendt, 1997; Fonseca and Cabral, 2007), it is natural to consider that early maturation may result in reduced fecundity, reduced growth, and/or increased natural mortality. In this study, we systematically explore the evolutionary impacts of fishing under all these scenarios.

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

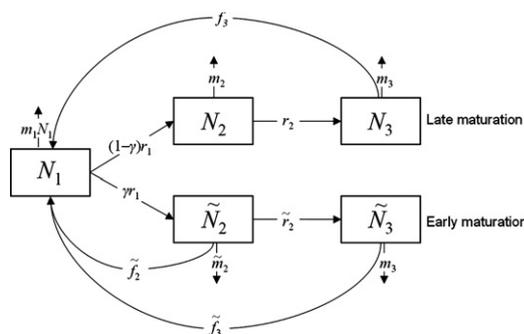
In the following sections, we investigate maturation evolution in a size-structured continuous-time model of a selectively harvested population. In particular, we extend previous analyses by systematically exploring the evolutionary implications of (1) different fitness costs of early maturation, which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

## 2. Model description

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

### 2.1. Life-history processes

Newborn individuals enter the first size class, grow into the second size class at rate  $r_1$ , and from there grow into the third size



**Fig. 1.** Schematic illustration of the size-structured continuous-time life-history model analyzed in this study. The harvested population is partitioned into small individuals (first size class, with density  $N_1$ ), intermediately sized individuals (second size class, with densities  $N_2$  and  $\tilde{N}_2$ ), and large individuals (third size class, with densities  $N_3$  and  $\tilde{N}_3$ ). Individuals can mature early (with probability  $\gamma$ , bottom row) or late (with probability  $1 - \gamma$ , top row). Quantities with a tilde refer to the early-maturing life-history. The probability  $\gamma$  of early maturation is evolving. The parameters  $r_1$ ,  $r_2$ , and  $\tilde{r}_2$  are growth rates;  $f_2, f_3$ , and  $\tilde{f}_2, \tilde{f}_3$  are fecundity rates;  $1/m_1$  is the carrying capacity of the first size class;  $m_2, \tilde{m}_2$ , and  $m_3$  are natural mortality rates; and  $h_2, \tilde{h}_2$ , and  $h_3$  are harvest mortality rates.

class. With probability  $\gamma$ , individuals mature when entering the second size class (early maturation); otherwise, they mature when entering the third size class (late maturation). Late-maturing individuals grow into the third size class at rate  $r_2$ , while early-maturing individuals grow into the third size class at rate  $\tilde{r}_2$ . Late-maturing individuals produce offspring at rate  $f_3$ , while early-maturing individuals produce offspring at rate  $\tilde{f}_2$  in the second size class and at rate  $\tilde{f}_3$  in the third. Late-maturing individuals experience mortality rates  $m_2$  and  $m_3$  in the second and third size classes, respectively, while early-maturing individuals experience the corresponding mortality rates  $\tilde{m}_2$  and  $m_3$ . Natural mortality in the first size class is density-dependent and of logistic type, with carrying capacity  $1/m_1$ . Harvesting is assumed to be density-independent and to occur in the second and/or third size classes, with rates of harvest mortality denoted by  $h_2$  (individuals in the second size class that are late-maturing and thus immature),  $\tilde{h}_2$  (individuals in the second size class that are early-maturing and thus mature), and  $h_3$  (individuals in the third size class, which are all mature). The densities of individuals are denoted by  $N_1$  (individuals in the first size class, which are all immature),  $N_2$  (individuals in the second size class that are late-maturing and thus immature),  $\tilde{N}_2$  (individuals in the second size class that are early-maturing and thus mature),  $N_3$  (late-maturing individuals in the third size class, which are all mature), and  $\tilde{N}_3$  (early-maturing individuals in the third size class, which are all mature). Quantities with a tilde always refer to the early-maturing life-history. Table 1 provides an overview of all model variables and parameters.

**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>	
$\gamma$	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

2.2. Life-history dynamics

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

$$\frac{dN_1}{dt} = \tilde{f}_2 \tilde{N}_2 + \tilde{f}_3 \tilde{N}_3 + f_3 N_3 - m_1 N_1^2 - r_1 N_1. \tag{1}$$

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

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

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

$$\frac{dN_2}{dt} = (1-\gamma)r_1 N_1 - m_2 N_2 - h_2 N_2 - r_2 N_2. \tag{2b}$$

From left to right, the terms represent growth from the first size class, natural mortality, harvest mortality, and growth into the third size class, respectively.

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

$$\frac{d\tilde{N}_3}{dt} = \tilde{r}_2 \tilde{N}_2 - m_3 \tilde{N}_3 - h_3 \tilde{N}_3, \tag{3a}$$

$$\frac{dN_3}{dt} = r_2 N_2 - m_3 N_3 - h_3 N_3. \tag{3b}$$

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

2.3. Life-history trade-offs

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

3. Evolutionary consequences of size-specific harvesting

To determine the fitness differences between early- and late-maturing individuals, we consider their basic reproduction ratio,  $R_0 = F_2 T_2 + F_3 T_3$ ,

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

3.1. Evolutionary invasion analysis

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 late-maturing individuals,

Table 2

Qualitative effects of early maturation on the fecundity and average time spent in the 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	$F_2 \uparrow T_2 \downarrow$	$T_3 \downarrow$

respectively, we see that early maturation is favored by selection if and only if  $R_0^1 > R_0^0$  (bang-bang control; Sonneborn and Van Vleck, 1965). In Appendix A, we show that this inequality is equivalent to

$$\tilde{D}_2 \tilde{f}_2 > r_2 D_2 D_3 f_3 - \tilde{r}_2 \tilde{D}_2 D_3 \tilde{f}_3, \tag{5}$$

where  $D_i$  denotes the average time that a late-maturing individual entering size class  $i=2, 3$  will remain in that size class. Likewise,  $\tilde{D}_2$  denotes the average time that an early-maturing individual entering the second size class will remain in that size class. The difference between  $D_i$  and  $\tilde{D}_i$  on the one hand, and  $T_i$  on the other, is that the former measure the average time an individual entering a size class will remain there, whereas the latter measure the average time a newborn individual will stay in size class  $i$  during the course of its life. Ineq. (5) can be interpreted as describing a trade-off between the fitness gains due to early maturation in the second size class and the fitness losses due to early maturation in the third size class that result from reduced fecundity rate, reduced growth rate, and/or increased natural mortality rate.

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

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

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

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

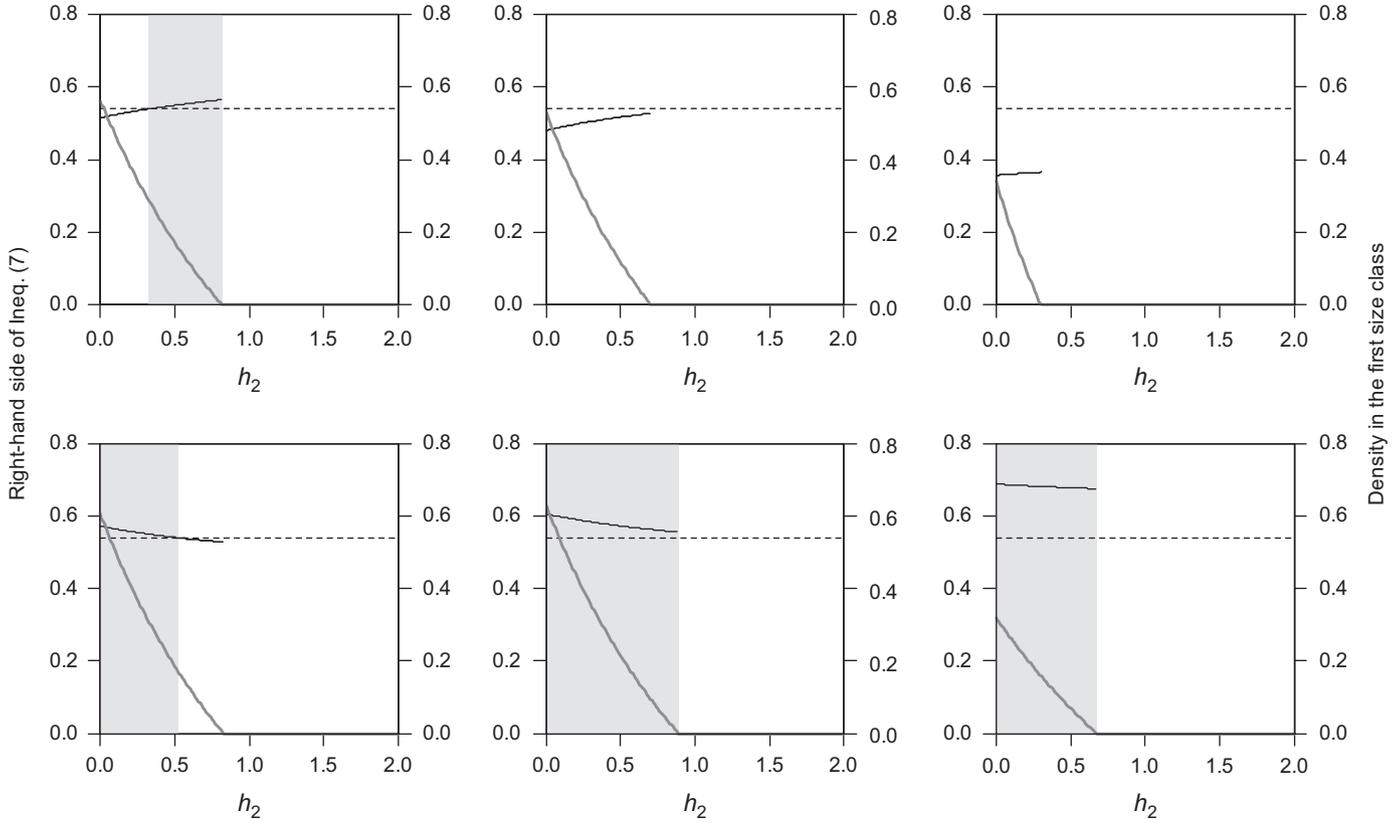
This inequality allows us to conclude that harvesting the third size class always promotes early maturation. The consequences of harvesting the second size class at a stage-unspecific rate  $h_2 = \tilde{h}_2$  are less obvious and are examined below for each of the three potential costs of early maturation.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

3.2. Trade-off between early reproduction and fecundity rate

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

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

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



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

3.3. Trade-off between early reproduction and growth rate

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

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

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

3.4. Trade-off between early maturation and mortality rate

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

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

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

3.5. Multiple trade-offs associated with early maturation

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

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

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

3.6. Conclusion

We have analyzed the effects of size-specific harvesting on maturation evolution for three potential costs of early maturation: reduced fecundity, reduced growth, and/or increased natural mortality. Results are summarized in Table 3: harvesting the smallest size class has no effect on maturation evolution, harvesting the intermediate size class can favor either early maturation (when mortality costs exceed growth costs) or late maturation (when growth costs exceed mortality costs), while harvesting the

largest size class always favors early maturation. As noted in Section 3.1, our analysis applies to the full parameter ranges in which the population remains extant. In Fig. 3, we demonstrate that each of the predicted outcomes does indeed occur.

#### 4. Evolutionary consequences of stage-specific harvesting

Using an analysis similar to that in the previous section, we can explore the effects of stage-specific harvesting, to examine the evolutionary consequences we expect from harvesting either

**Table 3**  
Evolutionary effects of increased harvest mortality rate. ↓ indicates that harvesting promotes early maturation, 0 indicates no effect, and ↑ indicates that late maturation is promoted. ↓/↑ indicates that harvesting promotes early maturation when the costs of early maturation are low, while late maturation is promoted when the costs of early maturation are high.

Harvesting of	Trade-off of early maturation with		
	Fecundity	Growth	Survival
Size class 1	0	0	0
Size class 2	0	↑	↓
Size class 3	↓	↓	↓
Immature individuals	↓	↓	↓
Mature individuals	↑/↓	↑/↓ or ↑*	↑/↓

\* When natural mortality in size class 2 exceeds that in size class 3, harvesting of mature individuals promotes late maturation independent of the growth costs of early maturation.

mature or immature individuals. This scenario applies when fisheries selectively target a stock’s spawning grounds or nursery grounds.

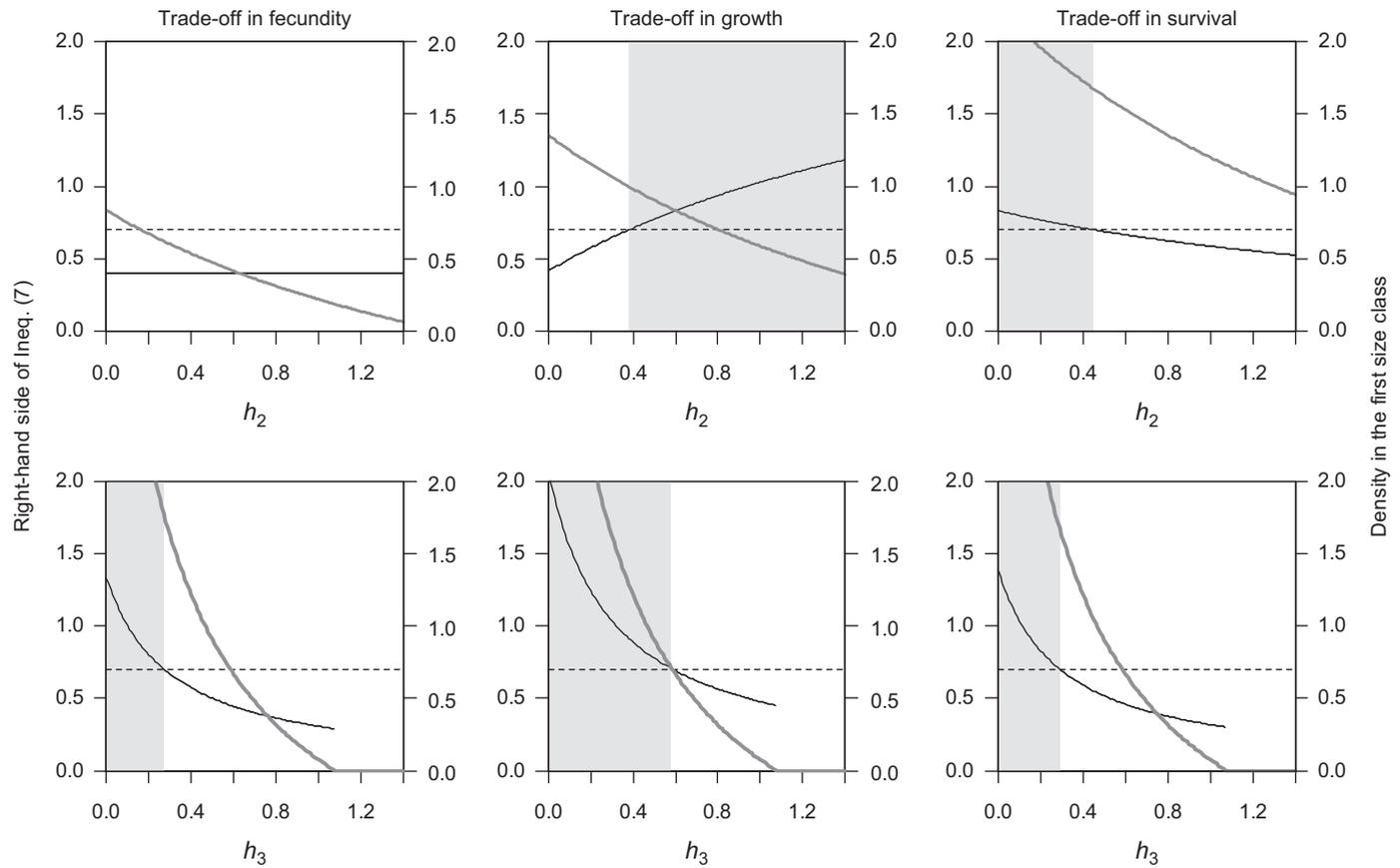
#### 4.1. Evolutionary invasion analysis

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

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

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

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



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

only if

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

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

#### 4.2. Trade-off between early reproduction and fecundity rate

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

#### 4.3. Trade-off between early reproduction and growth rate

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

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

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

#### 4.4. Trade-off between early maturation and mortality rate

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

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

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

#### 4.5. Understanding the evolutionary outcomes

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

When costs of early maturation are negligible and harvesting is absent, early- and late-maturing individuals have very similar life histories, which differ only in the additional offspring early-maturing individuals produce in the second size class. Evidently, early maturation hence is the better strategy, but its advantage

may be arbitrarily small. When mature individuals are harvested, this advantage is altered, since early-maturing individuals experience harvest mortality in both the second and the third size classes, whereas late-maturing individuals experience harvesting mortality only in the third size class. Provided that the advantage of early maturation is not too large in the absence of harvesting, the differential impact of harvesting mature individuals will thus tip the evolutionary balance in favor of late maturation. This tendency is already well known and understood.

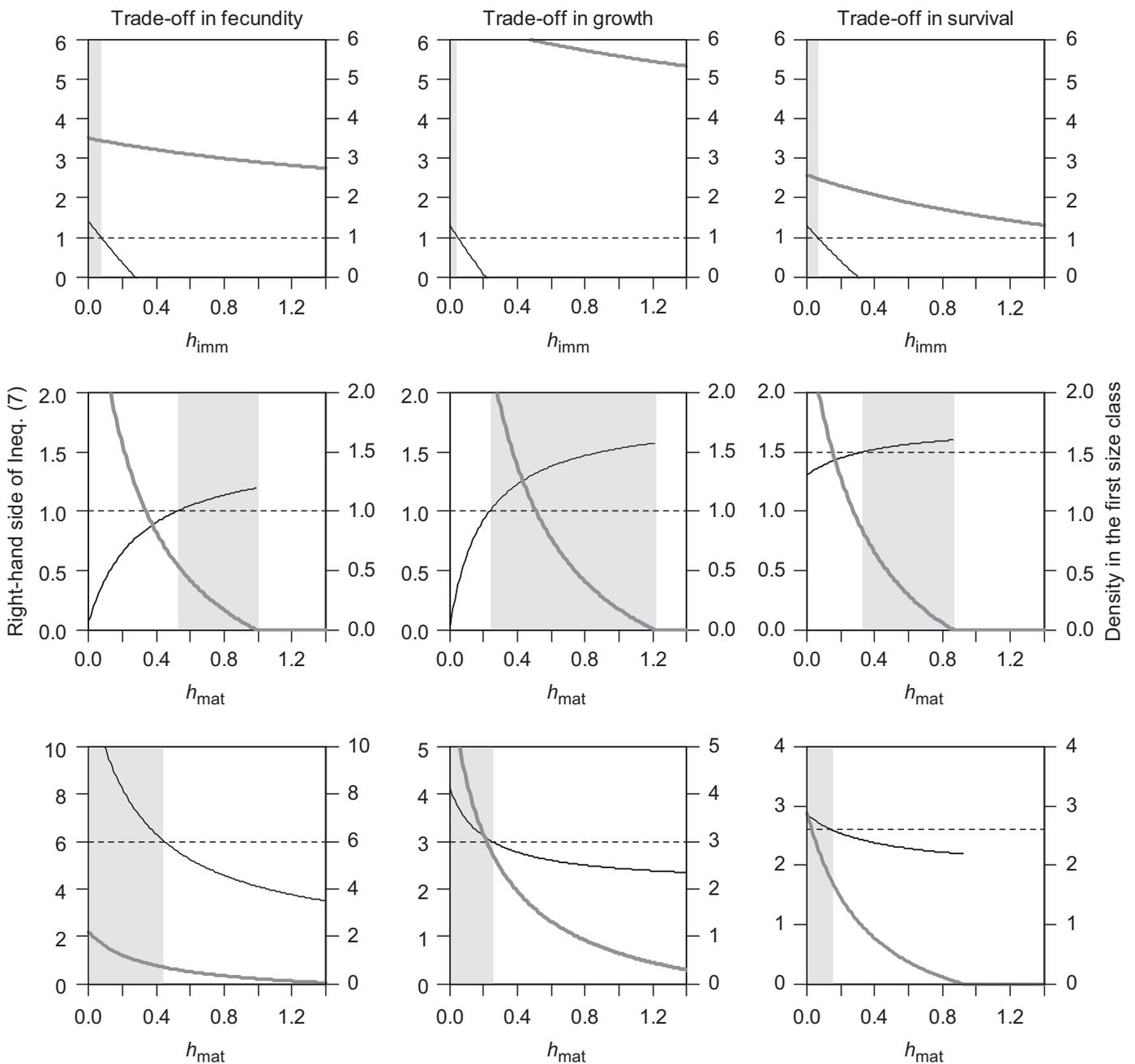
The reasons why harvesting mature individuals can induce early maturation when costs of early maturation are high are more subtle, and require appreciating two consequences of intensive harvesting: firstly, such harvesting makes it increasingly unlikely that early-maturing individuals reach the third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

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

When the trade-off between early maturation and growth rate is sufficiently strong, the growth of early-maturing individuals into the third size class is much impeded. If the natural mortality of late-maturing individuals is smaller in the third size class than in the second (Section 4.3), the expected duration that, in the absence of harvesting, late-maturing individuals spend in the third size class always exceeds that of early-maturing individuals in the second size class, which advantages late maturation. As the harvesting of mature individuals is increased, these durations become similar, so the aforementioned advantage of late maturation gradually disappears. At the same time, early-maturing individuals become unlikely to reach the third size class, whether they grow well or not, so the relative importance of the direct fitness cost of early maturation also gradually disappears. What remains is the natural evolutionary advantage of early maturation, which thus inevitably prevails once harvesting is intensive enough.

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

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



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

#### 4.6. Conclusion

We have analyzed the effects of stage-specific harvesting on maturation evolution for three potential costs of early maturation: reduced fecundity, reduced growth, and/or increased natural mortality. Results are summarized in Table 3. Harvesting immature individuals always favors early maturation. Harvesting mature individuals favors late maturation when the costs of early maturation are low. When natural mortality in the largest size class exceeds that in the intermediate size class, this conclusion remains true even when the growth costs of early maturation are

arbitrarily high. For all other cases, high costs of early maturation can reverse the evolutionary consequence of harvesting mature individuals, so that such harvesting then makes early maturation more advantageous. In Fig. 4, we demonstrate that each of the predicted outcomes does indeed occur.

#### 5. Discussion

Here we have analyzed harvest-induced maturation evolution under different costs of early maturation and for harvest regimes

with different selectivities. In particular, we have examined costs of early maturation that imply reduced fecundity, reduced growth, and/or increased natural mortality, while considering harvest regimes that are selective for either size or maturity stage. Our results provide a first systematic overview of how the evolutionary effects of harvesting vary with the trade-offs associated with early maturation and with the selectivities of harvesting regimes. The results of our investigation are summarized in Table 3, and paraphrased in Sections 3.6 and 4.5.

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

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

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

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

For harvesting to decrease the size at maturation, the direct fitness cost of early maturation must be large. As an example, when this cost is expressed in terms of higher natural mortality,

the harvesting of mature individuals may cause early maturation only if the additional mortality rate exceeds the natural mortality rate of the third size class. As another example, when the cost of early maturation is expressed in terms of lower growth, and natural mortality in the third size class is 10 percent lower than in the second, the harvesting of mature individuals may cause early maturation only if the early-maturing individuals grow 10 times slower than the late-maturing individuals. As a final example, when the cost of early maturation is expressed in terms of lower fecundity in the third size class, and the intrinsic growth and mortality rates are all equal, the fecundity must be reduced by half before harvesting mature individuals may cause early maturation.

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

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

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

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

Stage-specific fishing is common among stocks that undergo spawning migrations. Examples of such stocks include Northeast Arctic cod and Norwegian spring-spawning herring, where a strong spatio-temporal segregation of mature and immature fish enables targeted fisheries. Our results summarized in Table 3, for the “Harvesting of mature individuals”, are compatible with the maturation sizes observed for Northeast Arctic cod until about the middle of the 20th century, recognizing that these sizes were unusually large compared with all other stocks of Atlantic cod, that costs of early maturation are thought to be relatively low in this stock, and that the historical fishing regime had predominantly targeted mature individuals (Law and Grey, 1989; Jørgensen, 1990). Furthermore, our results summarized in Table 3, for the “Harvesting of immature individuals”, are compatible with the maturation sizes observed for Northeast Arctic cod since about the middle of the 20th century, recognizing that harvest mortality rates of immature Northeast Arctic cod in the Barents Sea has increased by a factor of approximately 5–7 from 1920 to 1960. Finally, our results summarized in Table 3, for the “Harvesting of mature individuals”, are compatible with the maturation sizes observed for Norwegian spring-spawning herring during the 20th century. For this stock, a marked decrease in growth after maturation indicates that the trade-offs between early maturation and growth, and thus also between early maturation and future fecundity, are strong (Engelhard et al., 2003). In accordance with our results, the evolutionary changes in size at maturation caused by intense harvesting on the spawning grounds of Norwegian spring-spawning herring have been found to be very small (Engelhard and Heino, 2004).

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

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## Appendix A. General invasion condition derived from basic reproduction ratio

An individual's basic reproduction ratio  $R_0$  equals its total lifetime reproductive output. For our model, this can be expressed as  $R_0 = F_2 T_2 + F_3 T_3$ , where  $T_2$  and  $T_3$  are the average times an

individual will spend in the two larger size classes, and  $F_2$  and  $F_3$  are the average fecundity rates in these size classes.

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

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

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

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

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

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

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

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

For  $R_0$ , we thus obtain

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

This is 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 reproduction ratios for early- and late-maturing individuals. Selection favors early maturation ( $\gamma=1$ ) 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 Eq. (A.5) to get

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

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

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

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

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

## Appendix B. Specific invasion conditions for harvesting mature individuals

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

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

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

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

$$f_3 - \tilde{f}_3 < \frac{f_3 m_3}{m_2 + r_2}. \tag{B.2}$$

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

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

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

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

$$\tilde{m}_2 - m_2 < m_3, \tag{B.5}$$

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

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

we obtain

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

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

$$\frac{\tilde{r}_2}{r_2} > 1 - \frac{m_3}{m_2}. \tag{B.7}$$

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

### Appendix C. Parameter values for numerical examples

The analyses presented in Sections 3 and 4 apply to the full parameter ranges for which the population persists, as illustrated in Fig. 2. In Figs. 3 and 4 we show that all predicted outcomes occur. To facilitate replication of these results, we provide in Table C1 the specific parameterizations that were used to produce each of the panels in Figs. 2–4.

**Table C1**

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

Panel	$m_1$	$m_2$	$\tilde{m}_2$	$m_3$	$r_2$	$\tilde{r}_2$	$\tilde{f}_2$	$f_3$	$\tilde{f}_3$
<b>Fig. 2</b>									
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 center	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 center	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
<b>Fig. 3</b>									
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 center	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 center	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
<b>Fig. 4</b>									
Top left	1.3	<i>0.60</i>	<i>0.60</i>	<i>0.60</i>	2.00	2.00	1.00	2.20	2.00
Top center	1.3	<i>0.40</i>	<i>0.40</i>	<i>0.20</i>	2.60	1.70	1.00	2.20	2.20
Top right	1.3	<i>0.30</i>	<i>0.60</i>	<i>0.20</i>	2.00	2.00	1.00	2.00	2.00
Middle left	1.3	<i>0.60</i>	<i>0.60</i>	<i>0.30</i>	2.00	2.00	1.00	2.20	2.00
Middle center	1.3	<i>0.40</i>	<i>0.40</i>	<i>0.20</i>	2.00	1.99	1.00	2.20	2.20
Middle right	1.3	<i>0.30</i>	<i>0.60</i>	<i>0.40</i>	2.00	2.00	1.50	2.00	2.00
Bottom left	1.3	<i>0.60</i>	<i>0.60</i>	<i>0.30</i>	2.00	2.00	6.00	2.00	0.10
Bottom center	1.3	<i>0.40</i>	<i>0.40</i>	<i>0.20</i>	8.00	0.10	3.00	2.20	2.20
Bottom right	1.3	<i>0.10</i>	<i>0.70</i>	<i>0.40</i>	2.00	2.00	2.60	2.00	2.00

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