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Life-history evolution in harvested populations: the role of natural predation

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ABSTRACT

Models and experiments of the evolution of age- and/or size-at-maturation in response to population harvesting have consistently shown that selective harvesting of older and larger individuals can cause earlier maturation. These predictions, however, are all based on single-species considerations and thus crucially neglect the selective forces caused or mediated by species interactions. Here we develop simple models of phenotypic evolution of age-at-first-reproduction in a prey population subject to different types of predation and harvesting. We show that, in the presence of natural predation, the potential evolutionary response of age-at-first-reproduction to population harvesting is ambiguous: harvesting can cause either earlier or later maturation depending on the type of predator interaction and its strength relative to the fishing pressure. The counterintuitive consequences of harvesting result from the indirect effects that harvesting of a prey population has on the selection pressure exerted by its natural predator, since this selection pressure itself typically depends on prey density. If harvest rates are high, the direct selection pressures considered in classical analyses prevail and harvesting decreases the age-at-first-reproduction, whereas at lower harvest rates the indirect, inter-specifically mediated effects of harvesting can qualitatively overturn predictions based on simpler single-species models.

Keywords: age-at-first-reproduction, age-at-maturation, age-specific mortality, density-dependent selection, fisheries-induced adaptive response, harvesting, life-history evolution, predation.

INTRODUCTION

The high mortality induced by population harvesting is one of the major environmental factors that may induce evolutionary change in exploited populations (Law and Grey, 1989; Brown and Parman, 1993; Stokes *et al.*, 1993; Heino, 1998). Size-selective harvesting, in particular, can cause adaptive responses in life-history traits related to body size such as size-at-age and age- and size-at-maturation (Edley and Law, 1988; Reznick *et al.*, 1990;

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Conover and Munch, 2002). Population harvesting occurs within commercial fisheries on a range of species and induces mortality at levels that well exceed natural mortality. Moreover, fishing mortality is often size-selective, especially when minimum mesh sizes are enforced. The evolutionary consequences of such large-scale exploitation are therefore a current concern (e.g. Browman, 2000; Law, 2000; Heino and Godø, 2002). Changes in size-related life-history traits can have drastic implications for both population persistence and yields (Edley and Law, 1988; Conover and Munch, 2002), and decreasing age- and size-at-maturation have already been documented in several exploited populations, such as North Sea plaice (*Pleuronectes plattesus*; Rijnsdorp, 1993), Northeast Arctic cod (*Gadus morhua*; Jørgensen, 1990), Baltic cod (*Gadus morhua*; Cardinale and Modin, 1999) and Atlantic cod (*Gadus morhua*; O'Brien, 1999). Although it has usually been impossible to unequivocally attribute these changes to adaptive responses (notable exceptions are Rijnsdorp, 1993; Heino *et al.*, 2002; Grift *et al.*, in press), evolution towards maturation at a younger age and/or smaller size in response to harvesting is consistently predicted by models (Law and Grey, 1989; Blythe and Stokes, 1993; Brown and Parman, 1993; Heino, 1998) and experiments (Edley and Law, 1988; Conover and Munch, 2002).

Until now, however, models of evolutionary responses to selective harvesting have largely focused on single species (Law and Grey, 1989; Blythe and Stokes, 1993; Brown and Parman, 1993; Heino, 1998). However, species obviously do not exist in isolation and species interactions, therefore, contribute to the selection pressures to which individuals must respond. This means that adaptive responses to extra mortality such as harvesting may be counteracted or reinforced by species interactions. Through interactions, the evolving species can, in turn, affect other species: evolution in one species' trait can feed back, via its effects on other species, on its further evolution. Selective forces that are both influencing and influenced by an evolving species constitute its so-called feedback environment (Dieckmann, 1997; Heino *et al.*, 1998; Meszéna and Metz, 1999). Its dimension – that is, the number of variables needed to describe the feedback environment in the dynamics of the evolving species – is crucial both for the choice of method for evolutionary analysis (Mylius and Diekmann, 1995) and for understanding life-history evolution (e.g. Heino *et al.*, 1997).

Incorporating the more complex feedback environment that results from species interactions into analyses of evolutionary responses to harvesting would be straightforward if the interspecific effects were independent of the evolving trait. In that case, there would be no feedback from the evolving species to the interacting species and back and, consequently, the dimension of the feedback environment would not change. Interspecific selection pressures would then remain constant in the course of evolution. Under such circumstances, there is no qualitative difference between the selection pressure resulting from natural predation and that resulting from population harvesting, and we simply recover the conventional predictions of increased mortality causing earlier maturation (Michod, 1979; Law and Grey, 1989). If, on the other hand, evolution in a focal species' trait affects its interactions with predators or competitors (for example, if the size-at-age of prey affects a size-selective predator), interspecific selection pressures become dynamic. Additional variables are then needed to describe the feedback environment of the focal species. Thus, the effect of increased mortality in the evolving species depends on the nature of its interspecific interactions: when these have to be included in the evolutionary analyses, responses of harvested populations become much harder to predict.

In this study, we address the effects of age-selective harvesting on the evolution of age-at-first-reproduction in a species that is subject to natural age-specific predation. We show that for such systems, conventional predictions about the evolutionary effects of harvesting can be qualitatively erroneous and that evolutionary outcomes turn out to be dependent on details of the predator–prey interaction. Below we develop and analyse models for prey populations that are subject to: (i) only age-selective harvesting; (ii) age-selective harvesting and predation by a predator not regulated by the prey; or age-selective harvesting and predation by a prey-dependent predator that feeds selectively on (iii) the youngest prey individuals, (iv) prey of intermediate age or (v) the oldest prey individuals.

EVOLUTIONARY RESPONSES TO HARVESTING IN A SINGLE SPECIES

We divide the harvested population into three age classes, one-year-olds ($i = 1$), two-year-olds ($i = 2$) and individuals aged three years or older ($i = 3$), all with age-specific survival probabilities s_i and fecundities f_i. Individuals can either start to reproduce as two-year-olds or as three-year-olds (i.e. $f_i = 0$). We let the second age class reproduce with a certain probability. This probability, denoted by γ, is the life-history trait or strategy variable we focus on throughout this paper. It is continuous and can take any value between zero and one, such that the extremes along this range correspond to maximally delayed ($\gamma = 0$) and expedited reproduction ($\gamma = 1$). In a population that is monomorphic for $\gamma = 0$, all individuals reproduce first when they have reached the third age class, whereas $\gamma = 1$ means that all individuals reproduce already at age two. (Throughout the paper, we use the term age-at-first-reproduction. Since we assume that mature individuals always reproduce, this is synonymous with the more common term age-at-maturation. For the same reason, we also use the terms delayed or expedited onset of reproduction.) The dynamics of population densities $N_{i,t}$ can then be described by

$$N_{1,t+1} = \gamma(f_2 N_{2,t} + \tilde{f}_3 N_{3,t}) + (1 - \gamma) f_3 N_{3,t} \tag{1a}$$

$$N_{2,t+1} = s_1 N_{1,t} \tag{1b}$$

$$N_{3,t+1} = s_2 N_{2,t} + s_3 N_{3,t} \tag{1c}$$

where time t is measured in years and s_2 and s_3 are survival probabilities, f_2 is the fecundity at age two, $\tilde{f}_3$ is the fecundity at age three and older for those individuals that start reproducing at age two, whereas f_3 is the fecundity at age three and older for those individuals that start reproducing at age three. We assume that fecundities and survival are size-dependent (Roff, 1992). Since we consider a constant size-at-age relationship, this results in age-specific fecundities and survival probabilities. Early reproduction is assumed to be costly, such that individuals reproducing at age two have a reduced fecundity at age three and onwards throughout their reproductive lives. The proportional reduction is measured by a cost $0 \leq c \leq 1$,

$$\tilde{f}_3 = f_3(1 - c) \tag{2}$$

To allow for population dynamics with stable equilibria without introducing a type of density-dependence that interferes with the evolving strategy, we let the survival s_1 from age one to two be density-dependent:

$$s_1 = \frac{s}{1 + mN_{1,t}} \tag{3}$$

where s is the density-independent survival probability and m is a constant that determines how strongly the survival of one-year-olds depends on density in this age class.

So far, we have only described the dynamics of a population characterized by a fixed life-history strategy γ. Our aim is to find the evolutionarily stable strategy (ESS; Maynard Smith and Price, 1973) for the probability γ of early maturation that cannot be invaded by any other strategy and also is evolutionarily attainable. We denote this strategy γ^*. For a quantitative trait under frequency-dependent selection ever to end up at an ESS, that strategy must be attainable through a sequence of small changes in the strategy (Eshel and Motro, 1981). An ESS that is also attainable in this manner is referred to as a continuously stable strategy, or CSS (Eshel, 1983). To find the CSS γ^*, we consider the fate of a variant with probability γ' of reproducing at age two appearing in a monomorphic population with the resident strategy γ. Assuming that the evolutionary dynamics in γ are slower than the ecological dynamics in N, the resident population can be assumed to be at its ecological equilibrium when the variant strategy arises. The variant's fitness $\lambda(\gamma',\gamma)$ is then given by the rare variant's initial population growth rate in the equilibrium environment determined by the resident strategy γ (following the definition of 'invasion fitness'; Metz *et al.*, 1992). If this invasion fitness exceeds one, the variant can invade the resident strategy and, except for exceptional circumstances, it also replaces the resident, thereby itself becoming the new resident (Geritz *et al.*, 2002). To find the invasion fitness, we thus need to know the feedback environment created by the resident and experienced by the variant strategy. As survival in our model is density-dependent, the feedback environment includes not only any extrinsic abiotic and biotic factors, but also the density of resident individuals. Including the latter explicitly, and assuming that the variant and the resident strategy share exposure to all other biotic and abiotic factors, the dynamics of the density N'_i of individuals with the variant strategy γ' is given by

$$N'_{1,t+1} = f_2\gamma' N'_{2,t} + f_3(1 - c\gamma')N'_{3,t} \tag{4a}$$

$$N'_{2,t+1} = \frac{sN'_{1,t}}{1 + m(N_{1,t} + N'_{1,t})} \approx \frac{sN'_{1,t}}{1 + mN_{1,t}} \tag{4b}$$

$$N'_{3,t+1} = s_2N'_{2,t} + s_3N'_{3,t} \tag{4c}$$

where the approximation in equation (4b) holds if the variant is rare. The survival of one-year-olds with the variant strategy then depends only on the density of juvenile individuals with the *resident* strategy γ – that is, $N_{1,t}$.

The invasion fitness $\lambda(\gamma',\gamma)$ is now given by the dominant eigenvalue of the linear dynamics in equations (4). Since we are only interested in whether or not the variant can invade, we can linearize the third-order polynomial for the eigenvalues λ around the threshold value $\lambda = 1$ by a Taylor expansion. The equilibrium density N_1^* of juvenile individuals with the resident strategy γ can be obtained from $\lambda(\gamma',\gamma) = 1$. The variant's invasion fitness is then given by

$$\lambda(\gamma',\gamma) = \frac{(\gamma' - \gamma)(f_2(1 - s_3) - f_3cs_2)(1 - s_3)}{(3 - 2s_3)(f_3s_2(1 - c\gamma) + f_2\gamma(1 - s_3)) - f_2\gamma'(1 - s_3)} + 1 \tag{5}$$

so that the invasion fitness exceeds one only if the ratio in equation (5) is positive. Analysis of the denominator shows that it does not influence the sign of the ratio, as long as the fecundity of two-year-olds is low or, when f_2 is higher, the changes in the evolving trait are not too large (see caption of Fig. 1). Focusing only on the numerator in equation (5), we thus conclude that a variant strategy with increased probability of reproducing at age two, $\gamma' > \gamma$, can invade if, and only if,

$$f_2 > \frac{cf_3 s_2}{1 - s_3} \tag{6}$$

There are thus two possible evolutionarily stable strategies: when inequality (6) is not fulfilled, the ESS is to always reproduce at age three ($\gamma = 0$), whereas when (6) is fulfilled, the ESS is to always reproduce at age two ($\gamma = 1$). These two evolutionary outcomes are illustrated by the pairwise invasibility plots in Figs 1a and 1b, respectively. Figure 1 also shows that any successfully invading variant, in turn, can be invaded by a variant even closer to the evolutionarily stable strategy, which therefore is a continuously stable strategy. Condition (6) is readily interpreted. It means that the strategy $\gamma' = 1$ of reproducing at age two is a CSS if, and only if, the benefit of reproducing early (that is, the fecundity f_2 of two-year-olds) exceeds the total costs of early reproduction. An individual that starts reproducing at age two suffers a reduced fecundity at age three and above (with the reduction amounting to cf_3). Since survival in the third age class decreases according to a geometric series, the average number of years during which the cost cf_3 is experienced is $(1 - s_3)^{-1}$. The probability that an individual will survive to reproduce as a three-year-old (and thus incur this cost of early reproduction) is s_2. The right-hand side of inequality (6) thus is the expected loss in fecundity *after* age two resulting from maturing early, whereas the left-hand side is the expected gain in fecundity *at* age two resulting from maturing early. Early maturation evolves when the gain exceeds the loss.

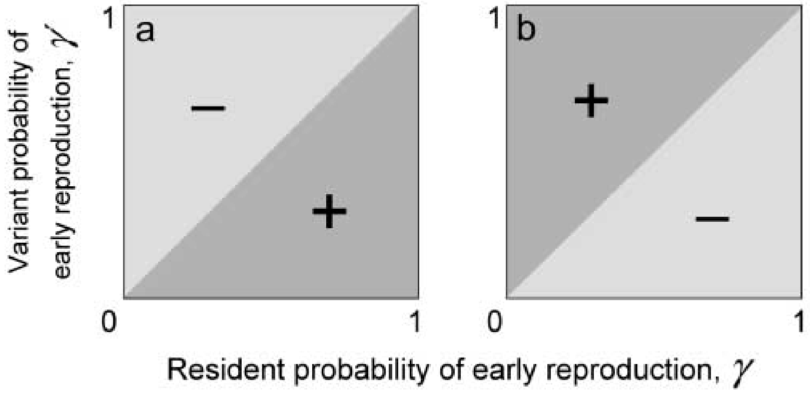

Fig. 1. Pairwise invasibility plots describing evolution of age-at-first-reproduction in an age-structured population subject to harvesting, in the absence of natural predation. Signs indicate for which combinations of the variant and resident probability of reproducing at age two, γ' and γ, the rare variant can invade the established resident population. Two evolutionary patterns are possible: either (a) all individuals delay reproduction until age three or (b) all individuals start reproducing at age two. These cases are distinguished by a threshold value for the fecundity of two-year-olds, given by inequality (8b). Evolutionary outcomes are the same for an unharvested population and for a harvested population that is subject to density-independent predation, with the threshold values then given by inequalities (6) and (8a), respectively. [Note that changes in the sign of the denominator in equation (5) may result in a small region of negative invasion fitness in the upper left corner of panel (b), which, however, remains without significance for the evolutionary outcomes.]

Inequality (6) implies that the higher the cost of early reproduction (c), the higher the fecundity at age two needs to be for early onset of reproduction to be a CSS. And, similarly, the higher the survival of either two- or three-year olds, the higher the fecundity of two-year olds needs to be for early reproduction to be a CSS. For a given life history (i.e. for given fecundities and natural survival probabilities), decreased survival of the intermediate or oldest age class (for example, due to population harvesting) makes the inequality more likely to be fulfilled. Thus, decreased survival favours the onset of reproduction at age two.

EVOLUTIONARY RESPONSES TO HARVESTING UNDER DENSITY-INDEPENDENT PREDATION

When the evolving population is both harvested and predated, the survival probabilities in equation (1) are products of natural survival, s^n, survival from harvesting and survival from predation. If harvesting removes a proportion h_i of individuals in age class i each year, the survival from harvesting at age i is given by $1 - h_i$. If harvesting occurs with a constant effort, this proportion is density-independent and constant between years. Similarly, if the predator population removes a proportion of age class i every year, the survival from predation in that age class is given by $1 - p_i$. The total survival probability at age i can then be written as

$$s_i = s_i^n(1 - h_i)(1 - p_i) \tag{7}$$

where the natural survival for age one remains density-dependent as described by equation (3). The age-specific per capita mortality due to predation, $0 \leq p_i \leq 1$, can be (and usually is) a function of predator density. If this predator density is independent of the densities of the prey, we can carry out the evolutionary invasion analysis as described above. We thus find that reproducing at age two ($\gamma' = 1$) is a CSS if, and only if,

$$f_2 > \frac{cf_3 s_2^n(1 - h_2)(1 - p_2)}{1 - s_3^n(1 - h_3)(1 - p_3)} \tag{8a}$$

By setting survival from predation to one in inequality (8a), we recover the condition for a single-species system (inequality 6), but now explicitly incorporate the effect of harvesting:

$$f_2 > \frac{cf_3 s_2^n(1 - h_2)}{1 - s_3^n(1 - h_3)} \tag{8b}$$

Thus, for all age- and size-dependent but density-independent harvest strategies, any increase in harvesting (h_2 or h_3) favours an earlier age-at-first-reproduction. Considering $p_i > 0$, we see from inequality (8a) that the effect of density-independent predation is the same as that of harvesting: evolution towards an earlier onset of reproduction. Moreover, the adaptive response to population harvesting in this type of two-species system is the same as in single-species systems: harvesting favours reproduction at age two. Even when predation and harvesting target different age classes – for example, if the predator selectively feeds only on two-year-olds and younger prey ($p_3 = 0$) while harvesting targets only the oldest individuals ($h_2 = 0$) – the adaptive response to harvesting is still fundamentally the same as in the single-species model. These evolutionary outcomes (late or early onset of reproduction) are illustrated by the pairwise invasibility plots in Figs 1a and 1b that correspond, respectively, to cases in which inequalities (8) are not fulfilled and are fulfilled.

EVOLUTIONARY RESPONSES TO HARVESTING UNDER DENSITY-DEPENDENT PREDATION

The threshold value for f_2 in inequality (8a) is only valid when predation is independent of the prey densities. If the dynamics of the predator instead depends on the prey (e.g. for growth, reproduction or survival), the per capita prey mortality from predation varies directly or indirectly with one or more prey densities. The probability of surviving predation then becomes a function of those densities, which, in turn, are functions of the evolving trait γ itself. In other words, the selection pressure from predation then dynamically depends on the evolving strategy.

In such circumstances, we need to specify how the predator density is affected by the prey and vice versa. The predator's effect on the prey depends, first, on how the predator's feeding rate is influenced by the prey density (functional response) and, second, on how a predation-induced decrease in prey density translates into an increase of predator density (numerical response). For analytical tractability, we assume these responses to be linear (type I according to Holling, 1959). If the predator feeds on all age classes of the prey with age-specific attack rates a_i, converts this energy to reproductive output according to an efficiency factor g, and experiences density-independent survival with probability l, the dynamics of the predator population are given by

$$P_{t+1} = gP_t\,(a_1N_{1,t} + a_2N_{2,t} + a_3N_{3,t}) + lP_t \tag{9a}$$

and the predation-induced per capita prey mortality in age class i is

$$p_i = a_iP_t \tag{9b}$$

Since these probabilities are limited to $0 \le p_i \le 1$, the range of predator densities for which the model is applicable is $0 \le P_t \le \min a_i^{-1}$. Outside of this range, and already close to its upper end, non-linear responses – resulting, for example, from a saturation of the predator's ingestion with increased prey density – can no longer be ignored.

Combining equations (9) with equations (1–3), the equilibrium densities for the three prey age classes and for the predator can be determined. To bring out the effects of predation on the different prey age classes as transparently as possible, we focus on cases involving predation on only one age class at a time. We treat the resulting three fundamental cases in turn.

In a system with density-dependent predation on only the youngest age class (i.e. $a_2 = 0$, $a_3 = 0$), the threshold value for f_2 is exactly the same as in the unpredated case and is thus given by inequality (8b). This is just as expected: all individuals, independently of whether they start reproducing as two- or three-year-olds, experience the same extra mortality imposed on the youngest age class during their first year of life. Therefore, the relative costs and benefits of reproducing early or late stays the same and the extra mortality is not involved in the threshold value for f_2. Thus, predation targeting only the youngest age class has no evolutionary consequences for age-at-first-reproduction.

EVOLUTIONARY RESPONSES TO HARVESTING IN A TWO-SPECIES MODEL: DENSITY-DEPENDENT PREDATION ON THE INTERMEDIATE AGE CLASS

When predation only occurs on two-year-olds (i.e. $a_1 = 0$, $a_3 = 0$), the viability of the prey and the predator populations depends on the relationship between the demographic parameters of prey and predator, including γ. The resulting equilibrium densities and viability conditions are presented in Appendix 1. The evolutionary invasion analysis of this system reveals that a variant with strategy γ' can invade if any of the three sets of inequalities (11) below is fulfilled. If

$$f_2 < \frac{ca_2g}{a_2gs(1-h_1) - m(1-l)} \text{ and } \gamma' < \gamma \tag{11a}$$

delaying the onset of reproduction to age three is the CSS. Instead, if

$$\frac{ca_2g}{a_2gs(1-h_1) - m(1-l)} < f_2 < \frac{a_2g}{a_2gs(1-h_1) - m(1-l)} \text{ and } \gamma' > \gamma \tag{11b}$$

reproduction at age two is the CSS. Accounting for all viability conditions in Appendix 1, inequalities (11a) and (11b) result in the two pairwise invasibility plots shown in Figs 2a and 2b. These are similar to the cases of no or density-independent predation presented in Figs 1a and 1b. However, the evolutionary outcome now depends not only on the demographic parameters of the prey, but also on those of the predator. In particular, increased attack rates, or enhanced growth or survival of the predator, cause earlier reproduction in the prey (Fig. 3a).

A third possibility for variant invasion arises if

$$f_2 > \frac{ca_2g}{a_2gs(1-h_1) - m(1-l)} \text{ and } \gamma' > \gamma \text{ and } \gamma < \hat{\gamma} \tag{11c}$$

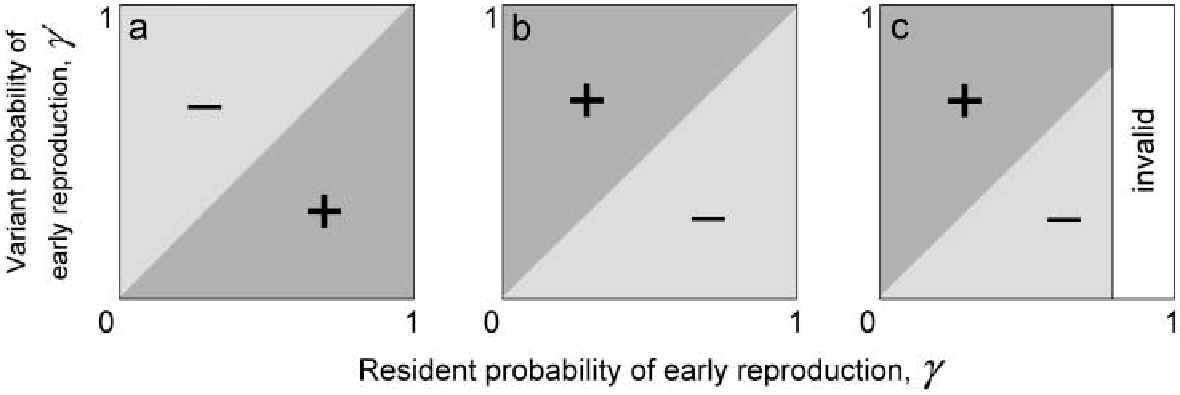

Fig. 2. Pairwise invasibility plots describing evolution of age-at-first-reproduction in an age-structured population subject to harvesting and density-dependent predation on the intermediate age class. Three evolutionary patterns are possible: (a) all individuals delay reproduction until age three, (b) all individuals start reproducing at age two, or (c) fecundities are so high that the predator population grows so large that no prey survive predation. In the latter case, the equilibrium densities of prey and predator underlying the evolutionary invasion analysis are no longer valid. These cases are distinguished by threshold values for the fecundity of two-year-olds, given by inequalities (11). The same evolutionary dynamics occur in a harvested population subject to density-dependent predation on its oldest age class, with the threshold values distinguishing the different cases then given by inequalities (12).

where

$$\hat{\gamma} = a_2 g / (f_2\,(a_2 g s(1 - h_1) - m(1 - l))) \tag{11d}$$

Then, variants with a higher probability of early reproduction can still invade, but for $\gamma \geq \hat{\gamma}$ the prey's probability to survive predation tends to zero and the model is no longer valid (Fig. 2c). This is because the combination of a very high fecundity of two-year-olds and a high probability of early reproduction results in such high production of prey that the predator can grow to very high densities because the predator has density-independent survival. Thus, the results of this invasion analysis based on a linear functional response are only applicable for $\gamma < \hat{\gamma}$. Population harvesting increases the range for which the model is valid because harvesting results in less food for the predator.

Inequalities (11) immediately show that harvesting of the youngest age class now tends to favour a *delayed* rather than expedited onset of reproduction (Fig. 3b): increased harvesting makes inequality (11a) less restrictive and thus causes a bias towards the case illustrated in Fig. 2a. The reason for this counterintuitive effect of harvesting is that harvesting decreases the interspecific selection pressure. Harvesting of one-year-olds diminishes the amount of food for the predators, which, in turn, reduces predator density and thus predation pressure on the prey population. By weakening the selection pressure exerted by the predator, harvesting of the prey species thus results in a delayed onset of reproduction.

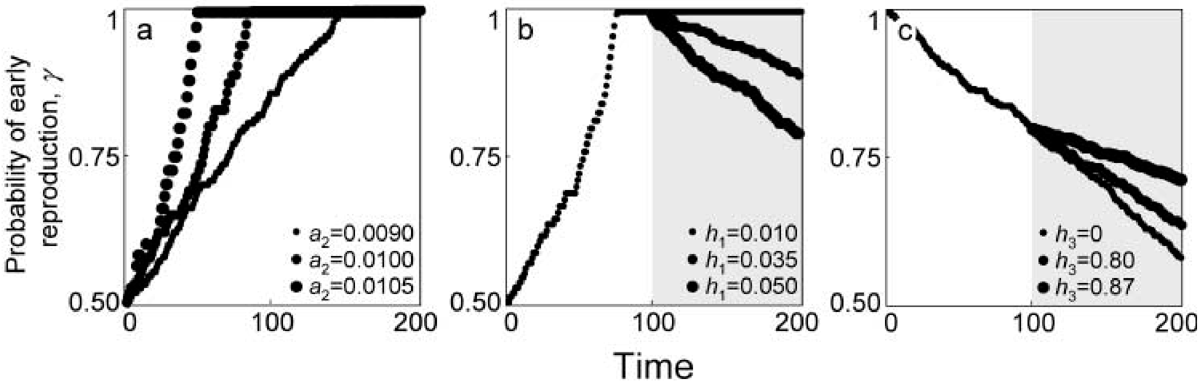

Fig. 3. Adaptive dynamics of the probability γ of early reproduction in a prey population subject to predation on its intermediate age class (a,b) and on its oldest age class (c). Adaptation occurs by the successful invasion of small random variations (drawn from a uniform random distribution, $0.98\gamma \leq \gamma' \leq 1.02\gamma$) that occur in the probability of early reproduction. The change in γ in the resident population is proportional to the selection gradient ($s = \partial\lambda'/\partial\gamma'$) multiplied by the amount of genetic variation σ_G^2 in the population. (a) Predation causes evolution towards an earlier onset of reproduction. Eventually the whole population starts reproducing at age two, $\gamma^* = 1$. The speed of adaptation increases with predation, measured by the attack rate a_2. (b) If the population (after having reached its continuously stable probability of maturation at $\gamma^* = 1$) is selectively harvested (indicated by grey shading) on the youngest age class, a delayed onset of reproduction is favoured, γ decreases, and the speed of evolution towards delayed reproduction increases with the strength of harvesting. (c) Harvesting can also increase the speed of evolution towards reproductive onset in the oldest age class in a population subject to predation on its oldest age class, which affects the strength of selection and thereby the speed of adaptation. Parameters: $a_1 = 0$, $c = 0.5$, $f_3 = 10$, $g = 0.5$, $h_2 = 0$, $l = 0.8$, $m = 0.01$, $s_1 = 0.5$, $\sigma_G^2 = 0.1$. (a) $a_3 = 0$, $f_2 = 7.5$, $h_1 = 0$, $h_3 = 0$, $s_2 = 0.5$, $s_3 = 0.5$. (b) $a_2 = 0.01$, $a_3 = 0$, $f_2 = 6$, $h_3 = 0$, $s_2 = 0.5$, $s_3 = 0.5$. (c) $a_2 = 0$, $a_3 = 0.01$, $f_2 = 4$, $h_1 = 0$, $s_2 = 0.8$, $s_3 = 0.8$.

Inequalities (11) further show that, with predation on the intermediate age class, harvesting of the intermediate or oldest age class does not affect the direction of selection, and thus also does not change the evolutionary outcome. The reason is that such harvesting does not remove any food from the predator and, therefore, has no indirect effect on the age-at-first-reproduction. Although it does not affect the direction of selection, harvesting of the oldest age class still influences the strength of selection (Table 1). Harvesting the oldest age class decreases the strength of selection for older age-at-first-reproduction and increases that for younger age-at-first-reproduction, although never to the extent that the direction of selection changes.

In summary, harvesting of a population subject to predation on its intermediate age class results in evolutionary responses that are quite different from those in systems with constant or no predation.

EVOLUTIONARY RESPONSES TO HARVESTING IN A TWO-SPECIES MODEL: DENSITY-DEPENDENT PREDATION ON THE OLDEST AGE CLASS

When the predator feeds on the oldest age class (i.e. $a_1 = 0$, $a_2 = 0$), the equilibrium densities of all prey age classes and the predator depend on the evolving trait γ. The prey age classes are viable for all values of γ, whereas the viability of the predator can be constrained by low or high limits of γ, depending on prey fecundities, as demonstrated in Appendix 2.

With the same simplifying assumptions as above, a variant with strategy γ' can invade if any of the three sets of inequalities (12) below is fulfilled. These inequalities allow for three types of evolutionary dynamics, the same types that occur when the intermediate age group is predated (Fig. 2). If the fecundity of two-year-olds is low, such that

Table 1. The effect of harvesting on the total strength of selection acting on age-at-first-reproduction in a predated population, based on the non-linearized selection gradient $s = \partial\lambda'/\partial\gamma$

Selectivity of predation	Direction of selection	Selectivity of harvesting		
		Age group 1	Age group 2	Age group 3
No predation	+79%	**0**[1]	**w** 1%, **s** 99%	**s**
	−21%	**0**[1]	**w**	**w** 83%, **s** 17%
Age group 1	+74%	**0**[1]	**w** 2%, **s** 98%	**s**
	−26%	**0**[1]	**w**	**w** 74%, **s** 26%
Age group 2	+96%	**w** 83%, **s** 17%	**0**[2]	**s**
	−4%	**w** 15%, **s** 85%	**0**[2]	**w**
Age group 3	+57%	**w**	**w** 4%, **s** 96%	**s**
	−43%	**w** 53%, **s** 47%	**w**	**w** 67%, **s** 33%

Note: The direction of selection is given by the sign of s: if $s > 0$ (indicated by +) younger age-at-first-reproduction evolves, whereas if $s < 0$ (indicated by −) older age-at-first-reproduction evolves. The sensitivity of the strength of selection to harvesting (defined as $\partial\,|\,s\,|\,/\partial h_i$) is calculated as an average over the range of γ for 100,000 parameter combinations that allow for co-existence of prey and predator populations. Parameter values were randomly drawn from uniform distributions over the biologically feasible range of each parameter. Harvesting weakens (**w**), strengthens (**s**) or has no effect (**0**) on the selection pressure.

[1] $\partial s/\partial h_1 = 0$. [2] $\partial s/\partial h_2 = 0$.

$$f_2 < \frac{c(a_3g + f_3m(1 - l))}{a_3gs(1 - h_1)} \text{ and } \gamma' < \gamma \tag{12a}$$

adaptation causes all individuals to delay first reproduction to age three (Fig. 2a). If, on the other hand, fecundity is higher, such that

$$f_2 > \frac{c(a_3g + f_3m(1 - l))}{a_3gs(1 - h_1)} \text{ and } \gamma' > \gamma \tag{12b}$$

adaptation causes all individuals to start reproducing as two-year-olds (Fig. 2b). However, if attack rate and survival of the predator are too high, such that

$$\frac{a_3g}{(1 - l)} > \frac{m}{s(1 - h_1)s_2^n(1 - h_2)}$$

the model is no longer valid for very high fecundity of two-year-olds. That is, if

$$f_2 > \frac{s_2^n(1 - h_2)(a_3g - f_3(1 - c)(a_3gs(1 - h_1)s_2^n(1 - h_2) - m(1 - l)))}{a_3gs(1 - h_1)s_2^n(1 - h_2) - m(1 - l)} \text{ and } \gamma < \gamma' < \hat{\gamma} \tag{12c}$$

variants with a higher probability of early reproduction can still invade, but the analysis is no longer valid for $\gamma \geq \hat{\gamma}$, with $\hat{\gamma}$ being given by equation (A9) in Appendix 2. This is because, similar to when there is predation on the intermediate age class, when two-year-olds have both a very high fecundity and a high probability of reproducing, the production of prey is so high that the predator population can reach very high densities (due to its density-independent survival). Thus, our evolutionary invasion analysis based on a linear functional response is only applicable for $\gamma < \hat{\gamma}$. The pairwise invasibility plots in Fig. 2 illustrate the general pattern observed. Note, however, that for some parameter combinations there are regions in the pairwise invasibility plots where either the harvested population or its predator is no longer viable. These additional cases are found by comparing inequalities (12) with the viability conditions in inequalities (A8) provided in Appendix 2.

The effect of harvesting on the onset of reproduction can be assessed directly from inequalities (12): harvesting of the youngest age class now favours adaptation towards later onset of reproduction (Fig. 4b), whereas harvesting of the intermediate and oldest age classes has no effect on the direction of selection (Fig. 4d). Again, these counterintuitive effects of harvesting on the age-at-first-reproduction are due to its impact on the selection pressure arising from predation. By harvesting the prey population, the predator population declines and, consequently, the selection pressure from predation (which alone causes an earlier onset of reproduction) decreases. When harvesting occurs on the youngest age class, this indirect effect of harvesting is strong enough to revert the direction of selection. When, instead, any of the two (potentially) reproducing age classes is harvested, the indirect effect is not strong enough to overcome the direct effect of these types of harvesting (which select for an earlier onset of reproduction) and, therefore, the direction of selection remains unaffected by harvesting the intermediate or oldest individuals. The effect of harvesting on the onset of reproduction in a population predated on its oldest age class (Figs 4b and d) is thus strikingly different from harvesting an unpredated population (Figs 4a and c).

Although harvesting of older individuals does not alter the direction of selection, all types of harvesting affect the strength of the total selection pressure (Table 1). The effect depends on the selectivity of both predation and harvesting. Harvesting of the youngest age

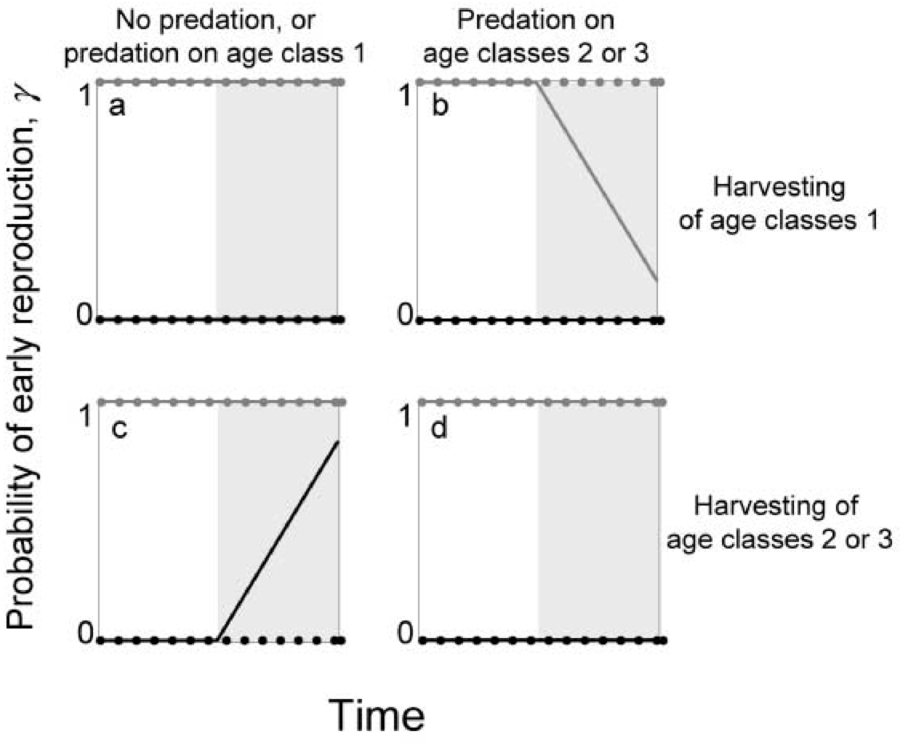

Fig. 4. Overview of how harvesting of the youngest age group (top row) or of the oldest age groups (bottom row) in populations subject to different types of predation affects the direction of selection on the probability γ of reproducing at age two. The prey population is allowed to stabilize at its evolutionarily stable probability γ^* before harvesting starts; when fecundity of two-year-olds is low (continuous lines) $\gamma^* = 0$ (i.e. the population starts reproducing at age three), whereas when two-year-old fecundity is high (dotted lines) $\gamma^* = 1$ (i.e. the population starts reproducing at age two). The period over which harvesting occurs is indicated by grey shading, and the harvest intensity can be either intermediate (grey lines) or strong (black lines). In the absence of predation, or for selective predation on the youngest age group, harvesting of the oldest age group can cause evolution towards earlier onset of reproduction (c), whereas there is no effect of harvesting of the youngest age group (a). If instead there is selective predation on the intermediate or oldest age group, harvesting of the oldest age group has no effect (d), and harvesting of the youngest age group can cause evolution towards later onset of reproduction (b). The schematic results shown here are based on simulations of the type presented in Fig. 3.

class weakens the selection pressure for earlier maturation, sometimes to the extent of causing an earlier onset of reproduction (Fig. 4b). Harvesting of the intermediate or oldest age class generally increases the strength of selection for younger age-at-first-reproduction, thereby inducing faster evolution of an early onset of reproduction. Similarly, such harvesting can also decrease the strength of selection for older age-at-first-reproduction and thus slow down the evolution of a late onset of reproduction (Fig. 3c). However, compared with when there is no predation or predation only on the youngest age class, harvesting of the intermediate age class now more often weakens the selection pressure for younger age-at-first-reproduction. Similarly, when there is predation on the oldest age class, harvesting of the oldest age class strengthens the selection pressure for older age-at-first-reproduction more often than when there is no predation or predation of the youngest individuals. As a consequence, harvesting of older individuals speeds up evolution towards older age-at-first-reproduction, and harvesting of the intermediate age class slows down evolution towards younger age-at-first-reproduction, more often than when there is no predation, because harvesting weakens the selection for younger age-at-first-reproduction from predation.

EVOLUTIONARY RESPONSES TO HARVESTING UNDER PREDATION WITH NON-LINEAR FUNCTIONAL RESPONSE

The results presented so far are all based on the assumption of a linear functional response in the predator. Assuming instead a non-linear functional response of Holling type II, the prey per capita mortality from predation in age class *i* and the predator population dynamics are given by

$$p_i = \frac{a_i P_t}{1 + b\sum_i e_i N_{i,t}} \tag{13a}$$

$$P_{t+1} = \frac{gP\,(a_1 N_{1,t} + a_2 N_{2,t} + a_3 N_{3,t})}{1 + b\sum_i e_i N_{i,t}} + lP_t \tag{13b}$$

respectively, where *b* determines how rapidly the predator reaches its maximum intake rate with increasing prey density and where e_i is the average energy content of a density unit of prey in age class *i*.

Assuming again small changes in the evolving trait as above, and exploring the outcomes of evolution in the reproductive strategy, we find that the qualitative results presented above hold also for a type II functional response: when there is prey-dependent predation on the intermediate or oldest age class, harvesting can select for a later start of reproduction. There is, however, one important difference: for parameters for which the predator's intake rate of prey is close to its maximum (that is, the denominator in the equations above is large), the prey's mortality from predation is essentially independent of its own density. The evolutionary responses to predation and harvesting are then the same as when predation is prey-independent, a case we have already analysed above.

DISCUSSION

Life-history traits that affect reproduction and sexual maturation are modified by various selection pressures, which are determined by the ecological context of the evolving species. In this paper, we explicitly accounted for a wider ecological context when studying the evolution of age-at-first-reproduction by including both a density-independent selection pressure (resulting from harvesting) and a density-dependent selection pressure (exerted by a predator). Based on simple phenotypic models, we have shown that, due to interactions between these selection pressures, the consideration of a larger feedback environment results in a wider spectrum of evolutionary responses than previously recognized. Depending on the relative strength of the density-dependent and -independent selection pressures, increased density-independent mortality can cause either evolution of earlier onset of reproduction, as predicted by previous single-species models based on more limited feedback environments (see, for example, Michod, 1979; Law and Grey, 1989; Blythe and Stokes, 1993), or evolution of delayed onset of reproduction.

The reversal of harvesting-induced adaptive responses by density-dependent selection pressures is most apparent when mortality is age-selective. When there is a single source of density-independent extra mortality and that mortality is age-selective, the only possible adaptive response in age-at-first-reproduction is towards a younger age-at-first-reproduction, even if there is an upper age limit to the extra mortality. This is because an individual cannot avoid ageing and thus cannot avoid the period of extra mortality – the only possibility is to reproduce before being killed. For simplicity, we have focused on age-selective mortality. Alternatively, mortality may be size-selective. For example, mortality due to commercial fishing is often both age- and size-selective (Law, 2000). If mortality is size-selective, an individual can influence the time of exposure to extra mortality through its body growth. Because of limited resources, there is a trade-off between body growth and reproduction, and the strategy of reproductive onset thus influences an individual's growth. After the onset of reproduction, body growth decreases and the time before reaching an upper size limit to the imposed mortality increases. Therefore, two responses to a single source of density-independent extra mortality on intermediate sizes are possible: individuals can either start reproducing at smaller sizes, before being killed, or delay reproduction to sizes larger than the upper size limit for the mortality, to maintain high body growth rate and thus rapidly traverse the size ranges exposed to a high mortality risk. This may result in alternative evolutionarily stable equilibria, as shown for harvest-induced changes in size-at-age (Ratner and Lande, 2001). However, size-specific harvesting could also have indirect effects mediated by prey-dependent species interactions. Further analysis of this commonly overlooked difference between age-specific and size-specific mortality (but see Roff, 1992) is particularly important in the context of interacting selection pressures like those investigated here.

The more diverse range of evolutionary outcomes that results from a more realistic feedback environment has important implications for assessing the evolutionary effects of human activities, especially of the large-scale commercial fishing industry that has emerged throughout the twentieth century. It has been shown that harvesting is expected to cause evolution of earlier maturation (Law and Grey, 1989; Blythe and Stokes, 1993; Heino, 1998). This prediction, however, can only be taken for granted for species that are largely unaffected by interactions with other species. More specifically, harvesting of old or intermediate-aged individuals always causes earlier maturation if (1) the target species is ecologically isolated, (2) the harvesting is overwhelmingly strong relative to any interspecific effects, or (3) the interacting species are unaffected by the harvested one. When, by contrast, the interacting species (fully or partially) depends on the harvested species, like the prey-dependent predator studied here, other adaptive responses to harvesting become possible.

The density-dependent selection pressures exerted by predation not only mediate the effect of the density-independent selection pressure from harvesting, they also determine which types of harvesting affect the evolution of maturation strategies. An important example is given by a harvesting strategy that targets the youngest age class of a population. Single-species models suggest that such harvesting has no effect on the evolution of age-at-first-reproduction, since the probability of surviving the juvenile period is equal for late-maturing and early-maturing individuals (Mylius and Diekmann, 1995). For harvested species that are predated, the situation is different: harvesting the youngest age class affects prey-dependent predators, thus decreasing mortality from predation at later ages, and thereby altering the selection pressures that govern the evolution of age-at-first-reproduction.

For all these conclusions, the relative magnitude of selection pressures resulting directly from harvesting and indirectly through interspecific interactions has to be considered. For example, in many commercially exploited fish species, fishing mortalities are so high (Hutchings, 2000) that the indirect evolutionary effects mediated by interacting species may be less important. In particular, the two species for which harvesting-induced genetic changes of declining age- and size-at-maturation have been suggested – North Sea plaice (Rijnsdorp, 1993) and Northeast Arctic cod (Heino *et al.*, 2002) – are both under heavy exploitation, with annual catches amounting to about 30% and 50%, respectively, of available biomass (ICES, 2001).

Recent concerns about the evolutionary consequences of large-scale exploitation in commercial fisheries (e.g. Browman, 2000; Law, 2000) have focused on empirical demonstrations of decreased age- and size-at-maturation. Our results show that a decreasing age-at-maturation is not the only evolutionary effect that can be expected from harvesting when the feedback environment includes relevant density-dependent mortality factors other than harvesting. Although here we have studied the effect of one such factor, predation, there are several other density-dependent causes of mortality that could mediate indirect evolutionary effects. Interspecific competition and cannibalism, common in the commercially important gadoid populations (Bax, 1998), are two examples.

Evolutionary effects like those discussed in this paper can also result from the interplay of different types of harvesting. For example, in populations exploited both by highly specialized and by relatively unselective fishing fleets, the fishing effort in the former depends on the density of the targeted species, whereas the effort in the latter is essentially density-independent. Interactions between density-dependent and -independent selection pressures are also important for understanding life-history responses to changes in factors other than harvesting, such as climate change or habitat destruction. When looking for, and explaining, adaptive responses of age- and size-related traits in exploited populations, care needs to be taken to accurately assess the appropriate feedback environment.

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APPENDIX 1: EVOLUTIONARY INVASION ANALYSIS FOR PREY-DEPENDENT PREDATION ON THE INTERMEDIATE AGE CLASS

In this appendix, we consider the case when $a_1, a_3 = 0$ and $a_2 > 0$ for a predator that depends on the prey for its existence and is affected by its density. The prey dynamics are described by substituting equations (7) and (9b) into (1–3), while the dynamics of the predator density are described by equations (9a). In this system, we obtain the following equilibrium densities:

$$N_1^* = \frac{1-l}{a_2gs(1-h_1) - m(1-l)} \tag{A1a}$$

$$N_2^* = \frac{1-l}{a_2g} \tag{A1b}$$

$$N_3^* = \frac{(1-l)(a_2g - f_2\gamma(a_2gs(1-h_1) - m(1-l)))}{a_2f_3g(1-c\gamma)(a_2gs(1-h_1) - m(1-l))} \tag{A1c}$$

and

$$P^* = \frac{(a_2gs(1-h_1) - m(1-l))(f_3(1-c\gamma)s_2^n(1-h_2) + f_2\gamma(1-s_3^n(1-h_3))) - a_2g(1-s_3^n(1-h_3))}{a_2f_3(1-c\gamma)s_2^n(1-h_2)(a_2gs(1-h_1) - m(1-l))} \tag{A2}$$

Substituting equations (A1), (7) and (9a) into equations (4), we can derive the invasion fitness of a variant with a probability γ' of reproducing early in a resident population with probability γ:

$$\lambda(\gamma', \gamma) = \frac{(\gamma' - \gamma)(f_2(a_2gs(1-h_1) - m(1-l)) - a_2gc)(1-s_3^n(1-h_3))}{(1-c\gamma)(a_2g(3-2s_3^n(1-h_3)) - f_2\gamma'(a_2gs(1-h_1) - m(1-l)))} + 1 \tag{A3}$$

As can be seen from equations (A1), the equilibrium prey densities, as formally derived, can sometimes be negative, which indicates that the prey population is not always viable. In particular, the youngest age class is only viable if

$$\frac{m}{s(1-h_1)} < \frac{a_2g}{(1-l)} \tag{A4}$$

This means that the youngest age class, and thus the prey population as a whole, is viable if the density-dependent decrease in prey survival, m, is sufficiently small relative to the density-independent survival, $s(1-h_1)$. The limit is set by the level of predation: the higher the predator's attack rate, growth rate or survival probability, the weaker the prey's density-dependence needs to be for it to survive. As can be seen from the numerator of equation (A1c), the oldest age class is only viable if $\gamma < \hat{\gamma}$, with $\hat{\gamma}$ given in (11d). This is because the survival probability of two-year-olds from predation, $(1-a_2P_t)$, becomes zero for $\gamma = \hat{\gamma}$ (see equations 7 and 9b). In reality, survival approaches zero asymptotically. In the limit in which the predator population consumes all prey individuals after their second year (at $\gamma \geq \hat{\gamma}$), so that the oldest age class of the resident population vanishes, it can be shown that the predator population will grow exponentially because of the density-independent survival of the predator population (see equation 9a). This can be seen by setting $(1-a_iP_t)$ and N_3^* in equations (1)–(3), (7) and (9) to zero, and solving for equilibrium densities. Thus, the evolutionary invasion analysis is applicable for $\gamma < \hat{\gamma}$, when all three prey age classes and the predator co-exist.

APPENDIX 2: EVOLUTIONARY INVASION ANALYSIS FOR PREY-DEPENDENT PREDATION ON THE OLDEST AGE CLASS

In this appendix, we consider the case a_1, $a_2 = 0$, $a_3 > 0$ for a predator that depends on the prey for its existence and is affected by its density. The equilibrium densities in this system are

$$N_1^* = \frac{f_3(1-c\gamma)m(1-l)(1+f_2\gamma s(1-h_1)) + a_3g(1-f_2\gamma s(1-h_1))^2 - (1-f_2\gamma \mathrm{s}(1-h_1))\sqrt{A}}{j(f_3(1-c\gamma)m(1-l) - a_3g(1-f_2\gamma s(1-h_1)) + \sqrt{A})} \tag{A5a}$$

$$N_2^* = \frac{f_3(1-c\gamma)m(1-l)(1+f_2\gamma s(1-h_1)) + a_3g(1-f_2\gamma s(1-h_1))^2 - (1-f_2\gamma s(1-h_1))\sqrt{A}}{f_2\gamma j(f_3(1-c\gamma)m(1-l) - a_3g(1-f_2\gamma s(1-h_1)) + \sqrt{A})} \tag{A5b}$$

$$\begin{aligned} N_3^* = (-\,2(1-l)(f_3(1-c\gamma)m(1-l)(1+f_2\gamma s(1-h_1)) + a_3g(1-f_2\gamma s(1-h_1))^2 - (1-f_2\gamma s(1-h_1))\sqrt{A}) \times \\ ((f_3(1-c\gamma)m(1-l) - a_3g(1-f_2\gamma s(1-h_1)) + \sqrt{A})(f_3(1-c\gamma)m(1-l) + a_3g(1-f_2\gamma s(1-h_1)) - \sqrt{A})^{-1} \end{aligned} \tag{A5c}$$

and

$$\begin{aligned} P^* = (-\,a_3gs_2^n(1-h_2)(1-f_2\gamma s(1-h_1)) + s_2^n(1-h_2)\sqrt{A}\, - \\ m(1-l)(f_3(1-c\gamma)s_2^n(1-h_2) + 2f_2\gamma(1-s_3^n(1-h_3))))(2a_3f_2\gamma m(1-l)s_2^n(1-h_3))^{-1} \end{aligned} \tag{A6}$$

where

$$A = f_3^2(1-c\gamma)^2m^2(1-l)^2 + 2a_3g(1+f_2\gamma s(1-h_1))f_3(1-c\gamma)m(1-l) + a_3^2g^2\,(1-f_2\gamma s(1-h_1))^2 \tag{A7}$$

The right-hand sides of equations (A5) are positive for all biologically feasible parameter values. The predator population is viable if its attack rate and survival are high, such that

$$\frac{a_3g}{1-l} > \frac{m(1-s_3^n(1-h_3))}{s(1-h_1)s_2^n(1-h_2)} \tag{A8a}$$

and if fecundity of two-year-olds is high. When the fecundity of two-year-olds is low, the predator is viable only for low probability of early reproduction:

$$f_2 < \breve{f}_2 \text{ and } \gamma < \breve{\gamma} \tag{A8b}$$

where

$$\breve{f}_2 = \frac{s_2^n(1-h_2)(a_3g(1-s_3^n(1-h_3)) - f_3(1-c)(a_3gs(1-h_1)s_2^n(1-h_2) - m(1-l)(1-s_3^n(1-h_3))))}{(1-s_3^n(1-h_3))(a_3gs(1-h_1)s_2^n(1-h_2) - m(1-l)(1-s_3^n(1-h_3)))} \tag{A8c}$$

and

$$\breve{\gamma} = \frac{s_2^n(1-h_2)(a_3g(1-s_3^n(1-h_3)) - f_3(a_3gs(1-h_1)s_2^n(1-h_2) - m(1-l)(1-s_3^n(1-h_3))))}{(f_2(1-s_3^n(1-h_3)) - cf_3s_2^n(1-h_2))(a_3gs(1-h_1)s_3^n(1-h_2) - m(1-l)(1-s_3^n(1-h_3)))} \tag{A8d}$$

or if

$$f_2 < \breve{f}_2 \tag{A8e}$$

Instead of going extinct, the predator population can also become too large. When the fecundity of two-year-olds is high and a large proportion of them are reproducing, such that $\gamma > \hat{\gamma}$ with

$$\hat{\gamma} = \frac{s_2^n(1-h_2)(a_3g - f_3(a_3gs(1-h_1)s_2^n(1-h_2) - m(1-l)))}{(f_2 - cf_3s_2^n(1-h_2))(a_3gs(1-h_1)s_2^n(1-h_2) - m(1-l))} \tag{A9}$$

the probability for prey to survive predation becomes zero in equation (7), whereas in reality survival approaches zero asymptotically. In the limit where the predator population consumes all prey individuals after their third year (at $\gamma \geq \hat{\gamma}$), it can be shown that the predator population will grow exponentially due to its density-dependent survival (see equation 9a). This can be seen by setting $(1 - a_iP_t) = 0$ in equations (1)–(3), (7) and (9), noting that $N_{3,t}$ now only refers to individuals of age three since all the older ones are eaten by the predator, and by solving for the equilibrium densities. Thus, the evolutionary invasion analysis is applicable for $\gamma < \hat{\gamma}$, when the prey can survive to become older than three years and co-exist with the predator.

All possible ecological outcomes can be found by comparing the viability conditions in inequalities (A8) with the thresholds on two-year-old fecundity obtained by solving $0 < \hat{\gamma} < 1$. The evolutionary outcomes of all these cases are found by comparing the resulting fecundity thresholds with those in inequalities (12): in all these cases, the evolutionary outcomes are either the general ones described in Fig. 2 or, for some combinations of fecundity of two-year-olds and of three-year-olds, contain regions of γ for which the probability for three-year-olds to survive from predation becomes zero (such that the model is no longer applicable) and/or regions of γ for which the predator goes extinct.