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Ernande, B., Dieckmann, U. and Heino, M.

IIASA Interim Report
November 2003

International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report **IR-03-058**

Adaptive Changes in Harvested Populations: Plasticity and Evolution of Age and Size at Maturation

Bruno Ernande (ernande@iiasa.ac.at)
Ulf Dieckmann (dieckmann@iiasa.ac.at)
Mikko Heino (mikko.heino@imr.no)

Approved by

Leen Hordjik
Director, IIASA

November 2003

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Contents

Abstract

We investigate harvest-induced adaptive changes in age and size at maturation by modelling both plastic variation and evolutionary trajectories. Harvesting mature individuals displaces the reaction norm for age and size at maturation toward older ages and larger sizes and rotates it clockwise, whereas harvesting immature individuals has the reverse qualitative effect. If both immature and mature individuals are harvested, the net effect has generally the same trend as when harvesting immature individuals only. This stems from the sensitivity of the evolutionary response that depends on the maturity state of harvested individuals, but also on the type of harvest mortality (negatively or positively density-dependent, density-independent) and the value of three life history parameters (natural mortality, growth rate, and the trade-off between growth and reproduction). Evolutionary changes in the maturation reaction norm have strong repercussions for the mean size and the density of harvested individuals that, in most cases, result in the reduction of biomass — a response that population dynamical models would overlook. These results highlight the importance of accounting for evolutionary trends in the long-term management of exploited living resources and give qualitative insights as to how to minimize detrimental consequences of harvest-induced evolutionary changes in maturation reaction norms.

About the Authors

Bruno Ernande
Adaptive Dynamics Network,
International Institute for Applied Systems Analysis,
Schlossplatz 1, A-2361 Laxenburg, Austria

Ulf Dieckmann
Adaptive Dynamics Network,
International Institute for Applied Systems Analysis,
Schlossplatz 1, A-2361 Laxenburg, Austria

Mikko Heino
Institute of Marine Research,
P.O. Box 1870 Nordnes,
N-5817 Bergen, Norway
and
Adaptive Dynamics Network,
International Institute for Applied Systems Analysis,
Schlossplatz 1, A-2361 Laxenburg, Austria

Acknowledgment

This research has been supported by the European Research Training Network ModLife (Modern Life-History Theory and its Application to the Management of Natural Resources), funded through the Human Potential Programme of the European Commission (Contract HPRN-CT-2000-00051). UD acknowledges financial support by the Austrian Science Fund (FWF), and by the Austrian Federal Ministry of Education, Science, and Cultural Affairs (BM:BWK)

Adaptive Changes in Harvested Populations: Plasticity and Evolution of Age and Size at Maturation

Bruno Ernande
Ulf Dieckmann
Mikko Heino

1. Introduction

Concern has recently grown about the fact that the exploitation of living resources not only entails demographic consequences for the target species but may also induce adaptive changes in their life history (Stokes *et al.* 1993; Palumbi 2001; Ashley *et al.* 2003). For instance, in commercially exploited fish stocks fishing is often the major source of mortality and hence must be expected to induce phenotypic adaptive responses (Policansky 1993; Conover 2000; Law 2000; Stokes & Law 2000; Heino & Godø 2002).

A central issue when dealing with harvest-induced adaptive changes is to distinguish between their evolutionary and plastic components (Reznick 1993; Rijnsdorp 1993; Law 2000). First, harvesting can alter the genetic composition of exploited populations by removing individuals selectively (Sheridan 1995), which may result in rapid life history evolution (Reznick *et al.* 1990; Conover & Munch 2002). Second, phenotypic plasticity allows individuals to quickly respond to harvest-induced alterations of environmental conditions (Policansky 1993; Trippel 1995; Rochet 1998; Law 2000). It has even been suggested that plastic responses may act as buffers against selective pressures, thus preventing evolutionary changes (see reviews by Stearns 1982 and Sultan 1987). Disentangling these two key components is particularly important because of their different management implications: mitigating adverse evolutionary changes takes many generations, whereas phenotypically plastic responses usually occur within a single generation (Reznick 1993).

Phenotypic plasticity can be characterized by reaction norms, which in turn are genetically determined. In other words, genotypes code for the set of phenotypes they plastically express across a given range of environments, namely their reaction norm (Schmalhausen 1949). Because of the high plasticity of many life history traits, genetic or evolutionary changes in exploited populations are best assessed by analysing

modifications in the corresponding reaction norms (Rijnsdorp 1993; Grift *et al.* 2003). By contrast, mere plastic adaptations displace expressed phenotypes along the reaction norm, without changing the reaction norm itself.

Statistical analyses of long-term data from some exploited fish stocks have already revealed evolutionary changes in reaction norms (Grift *et al.* 2003; Heino *et al.* 2002a, b). However, once such changes are demonstrated in exploited populations, identifying the responsible selective pressures becomes key to adjust management practices. Modelling the evolution of reaction norms then is indispensable: it allows identifying past selective pressures (natural and harvest-induced) that were responsible for the observed adaptive changes, and it permits predicting future changes based on current selective pressures.

This paper investigates the effect of harvesting on the evolutionary dynamics of reaction norms of age and size at maturation. Age and size at maturation are important life history traits influencing survival until maturity, subsequent reproductive effort and growth, offspring survival, the length of the reproductive life span, and thus expected lifetime fecundity (Roff 1992; Stearns 1992). Moreover, age and size at maturation are of specific interest in the context of exploited populations: since they affect the age and size composition of populations and thereby their reproductive potential (most animal species exhibit size-dependent fecundity and/or reproductive success), any change in these traits might indeed have strong repercussions for population dynamics and sustainable harvesting.

2. Model Description

(a) Life cycle and population dynamics

We consider a fairly general life cycle that is divided into three stages – larvae (*l*), juveniles (*j*), and adults (*a*) – connected by three transitions – metamorphosis, maturation, and reproduction (figure 1*a*). Individuals are distributed along a heterogeneous environment, which results in variation in somatic growth. We therefore characterize environments by their associated length-based growth rate, g. The distribution of individuals across environments changes with their life stage. First, larvae distribute randomly across environments because of limited moving capacity. After metamorphosis, individuals gain better mobility and thus can actively select their habitat. We assume that habitat choice occurs just after metamorphosis and that individuals settle in the chosen habitat for the remainder of their life. Individuals thus experience different environments during larval and juvenile-adult stages (illustrated by the thick arrows in figure 1*a*), which results in a growth trajectory (illustrated by the thin continuous lines in figure 1*b*) characterized by the growth rates (g_l, g_j) in the larval and juvenile-adult environment.

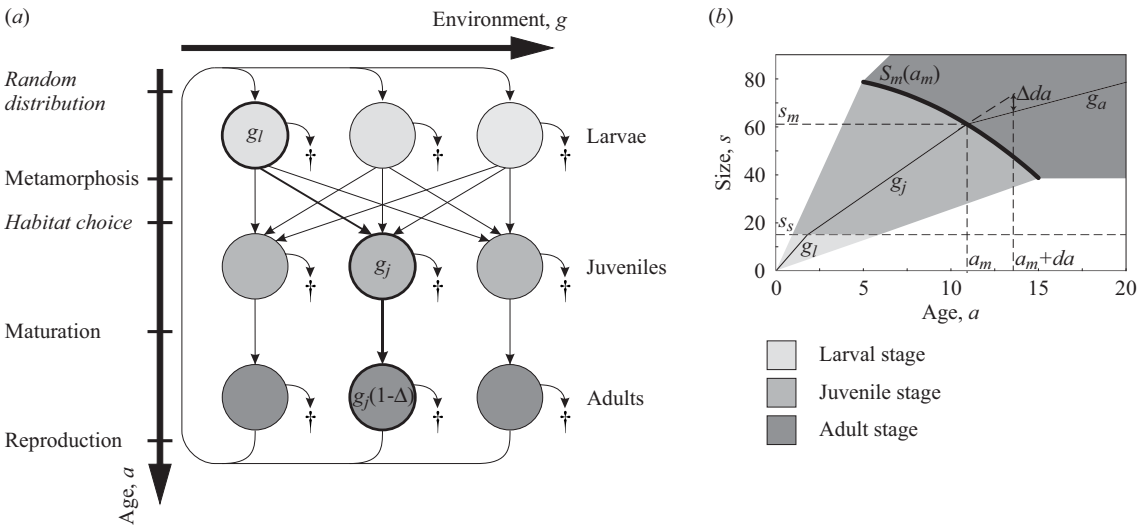

Figure 1. (*a*) Population life cycle. We consider a stage- and age-structured population in a heterogeneous environment. Individuals pass through three life stages (larvae, juveniles, and adults) and experience three transitions (metamorphosis, maturation, and reproduction). Thick arrows illustrate the life cycle of a single individual. (*b*) Somatic growth, metamorphosis, and maturation process. Growth rates g_l, g_j, and g_a apply during the larval, juvenile, and adult stages, respectively. Shaded areas represent the bundle of somatic growth trajectories resulting from environmental heterogeneity. Individuals metamorphose when their growth trajectory (thin continuous curve) reaches the fixed size at metamorphosis s_s (dashed horizontal line), and maturation occurs at the point (a_m,s_m) where the growth trajectory crosses the maturation reaction norm S_m (thick continuous curve). Thus, individuals metamorphose at different ages (but at fixed size s_s) and mature at different ages and sizes (a_m,s_m).

Length growth is supposed to be linear with age, with length affecting fecundity and (potentially) mortality. Larvae metamorphose into juveniles when they reach a fixed size threshold, s_s (figure 1*b*). By contrast, age a_m and size s_m at maturation are plastic as described by the maturation reaction norm, $S_m(a_m)$: maturation occurs when the juvenile growth curve intersects with the reaction norm (figure 1*b*). Mature individuals face an energy allocation trade-off between reproduction and somatic growth, captured by a reduced growth rate after maturation, $g_a = g_j(1-\Delta)$. Finally, per capita fecundity increases in proportion to body weight (i.e., to the cube of body length).

For many species, the larval stage is a critical period in terms of mortality and is largely responsible for population regulation (Charlesworth 1980; Wootton 1998). Recruitment of new larvae in an environment with growth rate g_l is given by a density-dependent function of Beverton-Holt type with an asymptotic carrying capacity $k(g_j)$. Natural mortality rates later in life depend on life stage and are assumed to be density-independent and given by m_l, m_j, and m_a. In addition, juveniles and adults may experience harvest mortality at rate h (referred to as harvest mortality throughout the rest of the text).

Assuming a certain maturation reaction norm $S_m(a_m)$, each individual is then characterized by three state variables: its age a and its growth trajectory (g_l,g_j).

Somatic growth being deterministic, size and thus stage and fecundity are fully determined by these state variables. Therefore, a continuous-time population model structured according to the three state variables (a, g_l, g_j) describes the population dynamics (Appendix A).

(b) Evolutionary trajectories

We describe the evolutionary trajectories of maturation reaction norms using adaptive dynamics theory (Metz *et al.* 1996; Dieckmann 1997; Geritz *et al.* 1998). Considering a population of resident individuals with a reaction norm S_m, we investigate whether a mutant with a new reaction norm S'_m can spread and invade in that population. Invasion by a mutant is possible if its invasion fitness f, computed as the expected long-term per capita growth rate of that mutant in an environment set by the resident population, is positive $f(S'_m, S_m) > 0$ (Metz *et al.* 1992; Rand *et al.* 1994; Ferrière & Gatto 1995; see derivation of fitness in Appendix B). We then describe long-term evolution of reaction norms as a sequence of substitutions during which residents are replaced by mutants with positive invasion fitness. For any phenotypic trait, and in the assumption of small mutational steps, the expected rate of such sequences is proportional to the selection gradient, the derivative of invasion fitness with respect to the mutant's trait (Dieckmann *et al.* 1995; Dieckmann & Law 1996). For an infinite-dimensional trait, like a reaction norm, we must consider the functional version of a derivative to obtain this selection gradient,

$$\mathrm{grad} f(S_m, a_m) = \frac{\partial}{\partial \varepsilon} f(S_m + \varepsilon \delta_{a_m}, S_m)\Big|_{\varepsilon=0}, \qquad (1)$$

where δ_{a_m} is the Dirac delta function peaked at a_m.

Most importantly, the selection gradient determines at any point $S_m(a_m)$, the direction of evolution relative to the current reaction norm: its value at a_m is positive if at that age an increase in size at maturation S_m is advantageous, and negative if this is deleterious. The evolution of the maturation reaction norm eventually stops when the selection gradient vanishes, $\mathrm{grad} f(S^*_m, a_m) = 0$, for every age a_m. We refer to these evolutionary end points S^*_m as evolutionarily singular (ES) reaction norms. Evolutionary singularities presented throughout the rest of the paper are evolutionary attractors that can be either evolutionarily stable (Maynard-Smith 1982) or evolutionarily unstable (so-called evolutionary branching points, Geritz *et al.* 1998).

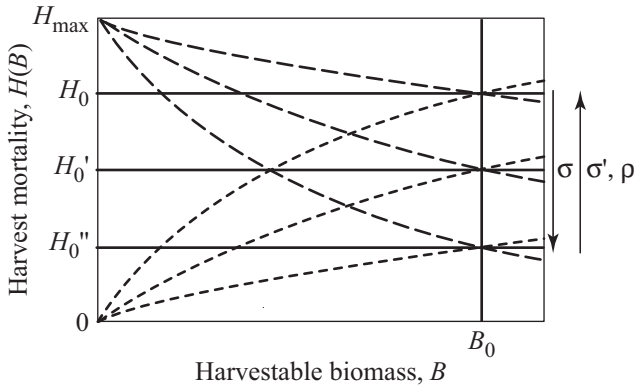

Figure 2. Variation of total harvest mortality with harvestable biomass for three alternative harvest mortality types. Negatively density - dependent $H(B) = H_{max} / (1 + \sigma \cdot B)$ (long - dashed curves), density-independent $H(B) = \rho$ (continuous curves), and positively density-dependent $H(B) = H_{max} \cdot (1 - 1/(1 + \sigma' \cdot B))$ (short-dashed curves) harvest mortalities are presented. For the sake of comparison, every population dynamic begins by harvesting on a previously unharvested population with biomass B_0; for a given scaling factor H_{max}, different values for initial harvest mortality H_0 are then obtained by adjusting σ, ρ, and σ', such that $H(B_0) = H_0$.

(c) Harvest mortality and management policies

Three management policies for determining annual catches are traditionally distinguished (Hilborn & Walters 1992). A policy of fixed quotas aims at constant annual catches, thereby creating negatively density-dependent harvest mortality. A policy of constant harvest mortality fixes the proportion of the population that is harvested, leading to density-independent mortality rate. Finally, a policy of fixed stock size keeps the biomass of the population after harvesting constant and, thus, generates positively density-dependent harvest mortality. Inspired by these classical schemes, we consider three possible types of harvest mortality $H(B)$ that differ in the way they relate to harvestable biomass (see figure 2 for details): (i) *negatively density-dependent harvest mortality* (which decreases as harvestable biomass increases); (ii) *density-independent harvest mortality* (which is independent of biomass); and (iii) *positively density-dependent harvest mortality* (which increases with harvestable biomass).

While the management policy determines harvest mortality $H(B)$ at the level of the whole population, the distribution of harvesting effort may still be heterogeneous across environments and result in variations in the locally experienced harvest mortality h. In particular, harvesting is expected to focus on environments where individuals are abundant and/or large. We thus assume that the harvesting effort η in an environment with growth rate g is proportional to the local harvestable biomass $\beta(g)$. In consequence, the local harvest mortality equals $h(g) = \eta(\beta(g))H(B)$ (Appendix C describes the computation of biomass B and harvesting effort η). Therefore, whatever the management policy is, harvest mortality is locally density-dependent.

3. Evolution of Maturation Reaction Norms in Harvested Populations

(a) Evolution under state-dependent harvesting

We first focus on situations in which either the juvenile or the adult part of the population is harvested, and refer to these as state-dependent harvesting. This may occur when the two life stages are physically segregated (resulting, e.g., from the migration of birds to reproduction areas, or from nursery and spawning areas in fish etc.). Such harvesting obviously modifies the ratio between juvenile and adult mortality rates.

Starting from the ES reaction norm for an unharvested population, figures 3*a* to 3*c* show, for the three harvest mortality types, the ES reaction norms evolving for increasing values of initial harvest mortality on adults. The observed effect is qualitatively the same in all three cases: as harvest mortality increases, the ES reaction norm evolves toward larger ages and sizes and turns clockwise, such that faster growing individuals mature larger and older. In contrast, harvesting on juveniles causes the reverse outcome: the ES reaction norm evolves toward lower ages and sizes and turns counter-clockwise as harvest mortality increases (not illustrated).

We define the sensitivity of the evolutionary response to harvesting as the average distance between the ES reaction norms for the unharvested and the harvested population, translating age differences into size differences according to the mean growth rate. Sensitivity differs according to the harvest mortality type and the life stage harvested.

Figure 3*d* shows that, as expected, sensitivity decreases from negatively to positively density-dependent harvest mortality with intermediate sensitivity for the density-independent case. Figure 3*e* illustrates that juvenile harvesting induces greater evolutionary changes than adult harvesting.

Furthermore, evolution of maturation reaction norms affects population density and mean size of individuals, both of which influence the harvestable biomass. As harvesting is here state-dependent, the part of the life cycle available to harvest shrinks (maturation occurring at younger and older ages for juvenile and adult harvesting, respectively), such that the density and, hence, the biomass of harvestable individuals diminishes. For juvenile harvesting, the effect on juvenile biomass is amplified by a decrease in juvenile mean size due to earlier maturation. In contrast, for adult harvesting, adult mean size increases because individuals mature larger and the trade-off between reproduction and growth is expressed later. This effect balances the decrease in adult biomass due to a reduction of adult life span.

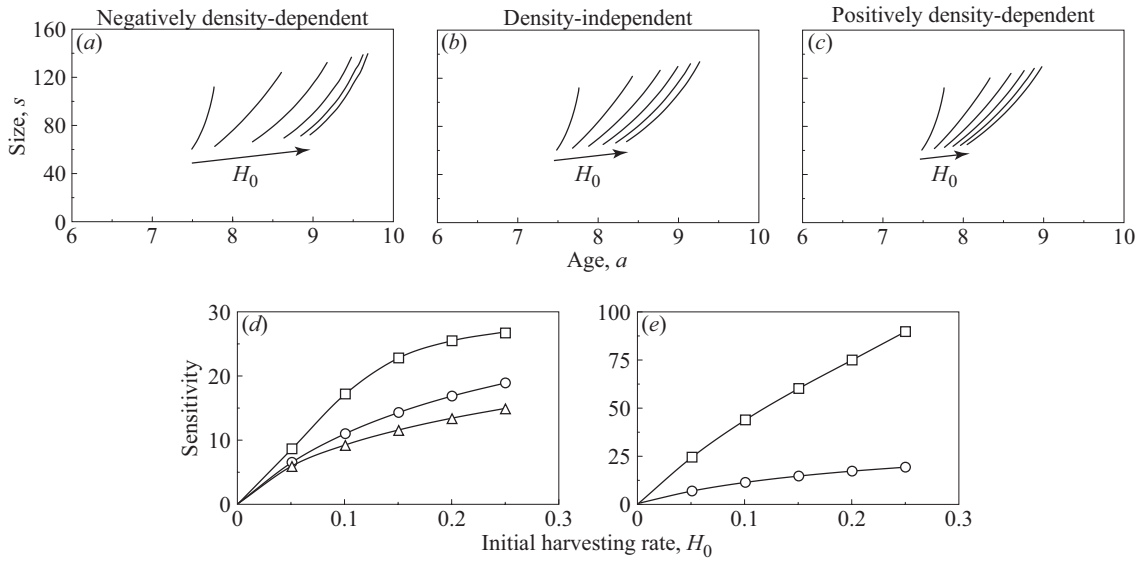

Figure 3. Evolution of maturation reaction norms under state-dependent harvesting. In this case, either juveniles or adults are harvested. Panels (*a*) to (*c*) present the ES reaction norms under increasing levels of initial harvest mortality on adults for the three harvest mortality types. In each panel, the initial harvest mortality, H_0, varies from 0 to 0.25 in steps 0.05. After harvesting has started, the harvest mortality may change because of density-dependence. (*d*) Sensitivity of the evolutionary response to harvest mortality types and changes in the value of initial harvest mortality. Squares, circles, and triangles correspond to negatively density-dependent, density-independent, and positively density-dependent harvest mortality, respectively. (*e*) Sensitivity of the evolutionary response to harvested life stages and changes in the value of initial harvest mortality. Squares and circles correspond to density-independent harvest mortality on juveniles and on adults, respectively. Other harvest mortality types produce the same qualitative results. Except when specified, parameters for this example and the subsequent ones are set as follow: size at metamorphosis $s_s = 5$, larval carrying capacity $k(g) = 25.10^6$, larval natural mortality rate $m_l(g) = 0.5$, juvenile and adult natural mortality rate $m_j(g) = m_a(g) = 0.3$, harvesting scaling factor $H_{\max} = 1$, trade-off strength $\Delta = 0.5$, fecundity scaling factor $\alpha_b = 2.10^{-5}$, weight scaling factor $\alpha_w = 1$, growth rates g are distributed normally $o(g) = N(12.5, 40)$, and habitat selection is made randomly $p(g) = o(g)$.

(b) Evolution under size-dependent harvesting

We now focus on management policies that prescribe a minimum harvesting size, irrespective of maturity state. Only individuals with lengths larger than $s_{\min}$ are harvested, leading to size-dependent harvesting. The position of the minimum harvesting size relative to the maturation reaction norm determines whether harvest mortality mostly affects only adults or both juveniles and adults.

Figures 4*a* to 4*i* depict, for the three harvest mortality types, the ES reaction norms for increasing values of initial harvest mortality and increasing minimum harvesting size. Again, implications are qualitatively the same for the three types of harvest mortality. Increasing harvest mortality displaces the ES reaction norm toward lower ages and sizes while turning it counter-clockwise, such that faster growing individuals mature larger and younger. Setting a minimum harvesting size implies that evolutionary changes almost stop as soon as the ES reaction norm lies below $s_{\min}$. Setting $s_{\min}$ closer

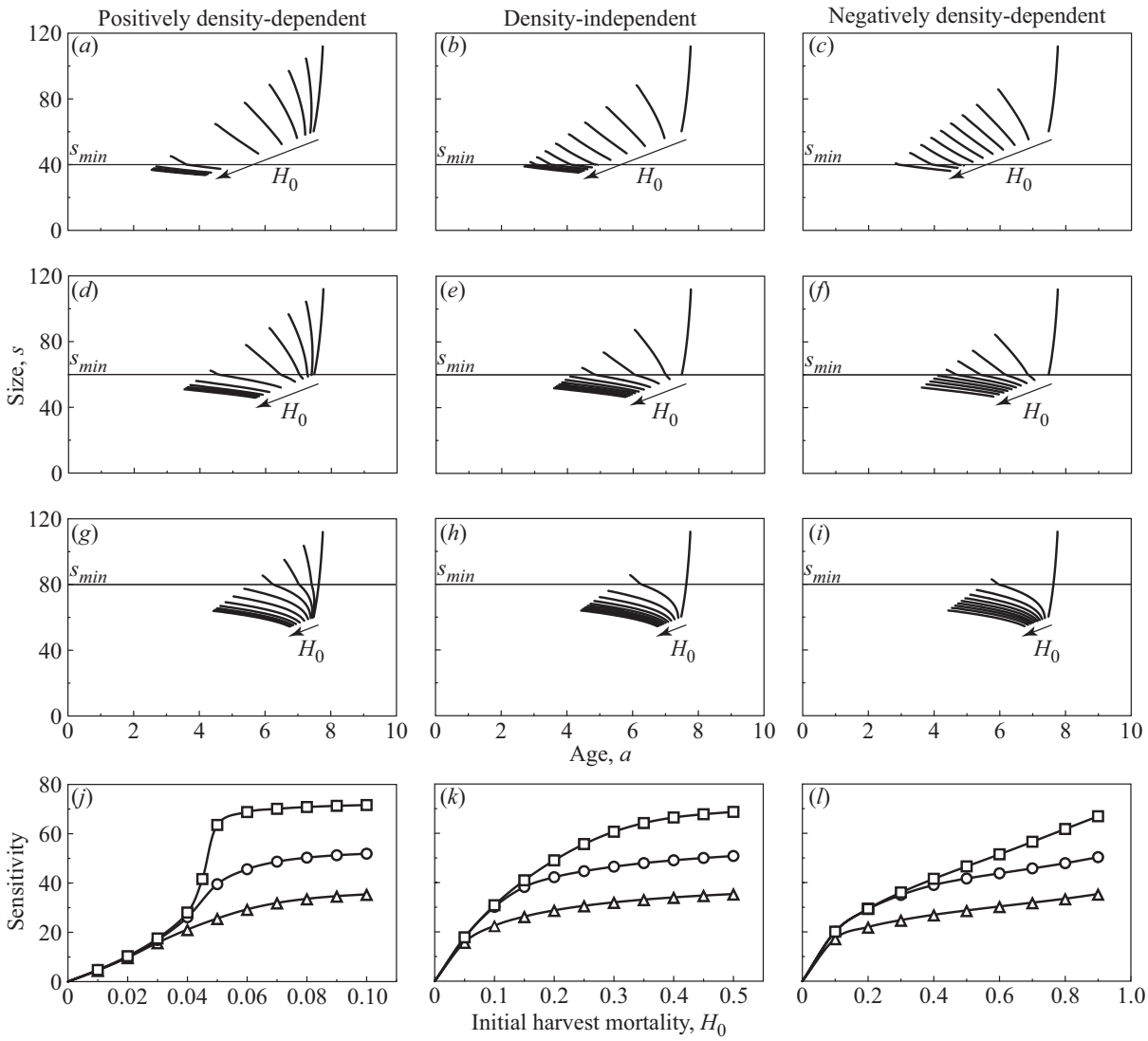

Figure 4. Evolution of maturation reaction norms under size-dependent harvesting. In this case, only individuals larger than the minimum harvesting size, $s_{\min}$, are harvested. Panels (*a*) to (*i*) show, for the three harvest mortality types and for increasing minimum harvesting size, the ES reaction norms for increasing levels of the initial harvest mortality. For negatively density-dependent harvest mortality, the initial harvest mortality, H_0, varies from 0 to 0.1 in steps of 0.01. For density-independent harvest mortality, the initial harvest mortality varies from 0 to 0.5 in steps of 0.05. For positively density-dependent harvest mortality, the initial harvest mortality varies from 0 to 0.9 in steps of 0.1. Panels (*j*) to (*l*) present the resulting sensitivity curves for the three harvest mortality types. Squares, circles, and triangles correspond to $s_{\min} = 40$, 60, and 80, respectively.

to the initial ES reaction norm thus reduces the evolutionary response to harvesting.

This latter result is illustrated by the sensitivity curves presented in figures 4*j* to 4*l*. Sensitivity levels off as initial harvest mortality reaches values for which the ES reaction norm lies below $s_{\min}$. In addition, the plateau value decreases as $s_{\min}$ is set closer to the initial ES reaction norm. We can again observe that sensitivity differs between harvest mortality types: when harvest mortality is negatively density-dependent, the plateau is reached for lower values of initial harvest mortality than when it is positively density-dependent, with the density-independent case giving intermediate results.

The fact that the maturation reaction norm evolves so as to lie just below the minimum harvesting size implies a decrease in ages and sizes at maturation if, as in our example, s_{min} is established below the maturation reaction norm. Smaller sizes at maturation induce a decrease in juvenile and adult mean size, reinforced, for adults, by an earlier expression of the trade-off between reproduction and growth. In consequence, the harvestable biomass declines.

(c) Differential consequences for population abundance

Figure 5 illustrates how consequences of evolutionary changes on population abundance differ across harvest mortality types by depicting changes in mean size, density, biomass, and harvest mortality over evolutionary time. The variables concern the harvested part of the population. Before evolution, the direct ecological (or demographic) effects of harvesting already diminish mean size, density, and biomass (dots on the vertical axes in figure 5). However, further changes result from evolution. As explained above, the maturation reaction norm evolves towards lower ages and sizes, so that mean size decreases over evolutionary time and biomass declines accordingly. For negatively density-dependent harvest mortality (figure 5*a*), the decrease in harvestable biomass induces an increase in harvest mortality. Consequently, the reaction norm evolves toward even lower ages and sizes, leading to further decreases in mean size, density, and, thus, biomass. In contrast, for density-independent harvest mortality (figure 5*b*), harvest mortality stays at a constant value, leading to a smaller decrease in biomass over evolutionary time. Finally, for positively density-dependent harvest mortality (figure 5*c*), the decrease in biomass induces a weaker harvest mortality, such that density increases during evolution. This partly compensates for the reduction of mean size, so that, over evolutionary time, the decline in biomass is smaller.

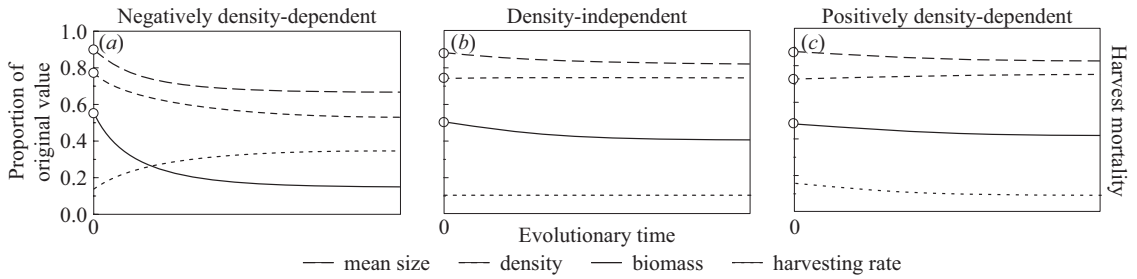

Figure 5. Consequences of maturation reaction norm evolution for population abundance. Panels (*a*) to (*c*) show, for the three harvest mortality types, changes in mean size, density, and biomass over evolutionary time (left y-axis). These variables refer to the harvested part of the population and are given as a proportion of their original values in an unharvested population. Harvesting is size-dependent with $s_{\min} = 40$; changes in the value of harvest mortality over evolutionary time are also shown (right y-axis). The ecological effects of harvesting are highlighted by open circles on the vertical axis of the panels: the more their position differs from 100%, the larger these effects. Initial harvest mortality is set so as to generate a decrease in biomass of about 50% before evolution**.**

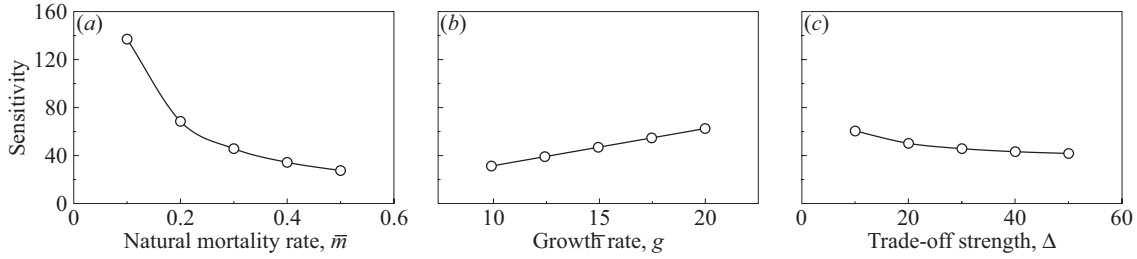

Figure 6. Life history parameters controlling the sensitivity of the evolutionary response. In these panels harvest mortality is density-independent and only affects juveniles. (*a*) Influence of natural mortality rate, $\bar{m}$. In this case, juvenile and adult natural mortality rates are equal, $m_j = m_a = \bar{m}$, and constant across environments. For any value of $\bar{m}$, the harvest mortality is set to 1/3 of juvenile natural mortality rate. (*b*) Influence of average growth rate, $\bar{g}$. For any value of $\bar{g}$, the coefficient of variation of growth rate across environments is 0.5, and the harvest mortality applied to juveniles is set to 0.1. (*c*) Influence of the trade-off strength between growth and reproduction, Δ. For any value of Δ, the harvest mortality applied to juveniles is set to 0.1.

(d) Sensitivity of the evolutionary response to harvesting

Our analysis shows that the sensitivity of the evolutionary response to harvesting is controlled by three life history parameters (Figure 6). The value of harvest mortality being fixed, sensitivity increases (i) as the average natural mortality decreases (figure 6*a*), (ii) as the average growth rate increases (figure 6*b*), and (iii) as the trade-off between growth and reproduction weakens (figure 6*c*). Note that natural mortality influences sensitivity much more strongly than the two other traits. These results imply that the maturation reaction norms of species characterized by high natural mortality, slow growth, and a strong trade-off between growth and reproduction are expected to be relatively immune to harvest-induced evolution, whereas species with low natural mortality, fast growth, and a weak trade-off should be particularly sensitive.

4. Discussion

This paper investigates harvest-induced adaptive changes in age and size at maturation by accounting for both plastic variation and evolutionary responses. We have shown how harvesting acts as a selective pressure displacing and shaping the reaction norm for age and size at maturation.

First, the position of the maturation reaction norm is predicted to change according to the maturity state of harvested individuals. Harvesting mature individuals induces later ages and larger sizes at maturation, whereas harvesting immature individuals induces younger ages and smaller sizes. When harvesting both immature and mature individuals (e.g., by setting a minimum harvesting size below the maturation reaction norm), the net evolutionary effect is, in most cases, a decrease in ages and sizes at maturation, because of the higher sensitivity of the evolutionary response to harvesting of immature individuals. These results generalize those obtained by Law & Grey (1989) and Heino (1998) for fixed age and size at maturation to plastically varying age and size at maturation. It actually appears that plastic variation does not qualitatively modify or even impede general trends in the evolutionary response of age and size at maturation to harvesting, contrary to a hypothesis often mentioned in the classical literature about phenotypic plasticity (see reviews by Stearns 1982 and Sultan 1987).

Second, the shape of the maturation reaction norm is also predicted to evolve according to the maturity state of harvested individuals, turning clockwise when adults are harvested and counter-clockwise when juveniles are harvested. Again, due to differential sensitivity, harvesting both adults and juveniles induces the same qualitative net effect as harvesting juveniles. The ‘tilting’ in the maturation reaction norm originates from the distribution of harvesting effort across environments. In the presented model, harvesting is more severe in environments with high biomass, so that, on average, fast growing individuals suffer from higher harvest mortality. In consequence, the harvesting pressure becomes stronger when moving along the reaction norm toward higher growth rates. The resulting differential selection pressure along the reaction norm causes the change in shape. Notice that in our study the ES reaction norm for unharvested populations is almost vertical, corresponding to maturation at a fixed age. It can be shown that this outcome only occurs if, as in our case, natural mortality does not vary across environments. This is of course not very likely in natural settings and vertical reaction norms should rarely be observed in the wild. However, this simplifying assumption allows us to transparently disentangle the effect of harvest mortality from other effects induced by natural mortality. In addition, it turns out that the direction of change in the slope of reaction norms is the same whatever the ‘natural’ ES reaction norm (results not shown).

Other limitations of our approach have to be noted. First, genetic details were traded off against ecological realism. Therefore, genetic constraints such as the lack of additive

genetic variance or genetic correlations between different points of the reaction norm, or between the reaction norm and other life history traits, are not considered. Second, in order to simplify the analysis, some biological aspects were not considered. Most importantly, we have ignored potential compensation in somatic growth, which could arise through density-dependent processes (Lorenzen & Enberg 2002), and potential concomitant harvest-induced evolution of life history traits, such as growth (Conover & Munch 2002). Both could affect, at least quantitatively, the evolution of maturation reaction norms and its consequences on population biomass. We have also considered maturation to be deterministic, whereas it is in essence a probabilistic process (Heino *et al.* 2002a, b). However, results of this study should qualitatively apply to probabilistic reaction norms, at least when maturation stochasticity is not too large. Finally, the simplifying assumption of a fixed habitat after metamorphosis may not apply to every organism. Very mobile species may experience more than two environments during their life cycle, thus experiencing higher variation in growth trajectories and mortality histories.

An important feature of the presented model is the use of infinite-dimensional traits, which are very handy to describe reaction norms, as well as a variety of other quantitative traits, e.g., growth trajectories and body shape (Kirkpatrick & Heckman 1989; Gomulkiewicz & Kirkpatrick 1992). An important advantage of an infinite-dimensional description of reaction norms is that it does not artificially constrain them, allowing any shape to evolve. In this context, it is worth highlighting that maturation at a fixed age (vertical reaction norm) or at a fixed size (horizontal reaction norm) only appear as specific cases in our model. In fact, as soon as both growth and mortality vary across environments, predicted reaction norms imply plasticity in both age and size at maturation. These results are consistent with previous theoretical findings (Stearns & Crandall 1984; Stearns & Koella 1986) and with the fact that both maturation at fixed age and fixed size are actually rare in nature (Bernardo 1993).

Earlier models of reaction norm evolution have assumed that one point of the maturation reaction norm corresponds to a single environment (Stearns & Koella 1986; Kawecki & Stearns 1993; Berrigan & Koella 1994). Our model overcomes this simplification by allowing several environmental trajectories and, thus, several growth and mortality histories, to reach the same point of the reaction norm. This may generate different or even antagonistic selective pressures that add up to determine the actual evolution of the reaction norm. Accounting for this fact improves the realism of the model, both in describing the pre-maturation process and in predicting the evolution of maturation reaction norms.

The repercussions of harvest-induced evolution in maturation reaction norms for population abundance highlight the need for considering evolutionary trends in the responsible long-term management of exploited populations. We have shown that the

mean size and density of individuals might change in the course of evolutionary responses, in most cases substantially reducing population biomass. Remarkably, this effect occurs on top of the immediate ecological response to harvesting. For instance, Figure 6*a* shows a decrease in biomass, relative to the unharvested situation, of about 45% at ecological equilibrium, whereas the reduction is as large as 85% at evolutionary equilibrium. Only models that consider both ecological and evolutionary feedback loops can describe such effects (Metz *et al*. 1992).

Our results provide insight into management options that could be used to mitigate the evolutionary consequences of harvesting. First, not surprisingly, management policies that cause harvest mortality to decrease with biomass (i.e., positively density-dependent harvest mortality), result in lesser evolutionary responses than policies generating other harvest mortality types. Second, in line with some earlier results (Law & Grey 1989; Heino 1998), selective harvesting of mature as opposed to immature individuals is evolutionarily preferable if the objective is to avoid evolution towards earlier maturation. Third, harvesting with a minimum allowable size set such that immature individuals are mostly below the size limit would minimize evolutionary changes in maturation. The latter result contradicts a recommendation by Conover & Munch (2002) who suggested that in order to prevent harvest-induced decay in somatic growth, it is the harvesting of the largest individuals that should be avoided. This qualitative difference highlights that minimizing selection on one trait might increase selection on another trait. In the longer term, therefore, models ought to be developed allowing for an integrative assessment of harvest-induced selection.

To conclude, we highlight the general relevance of our results for the evolutionary ecology of maturation reaction norms. First, plasticity in the maturation process does not act as a buffer against selective pressures arising from changes in the general mortality regime. Second, position and shape of the maturation reaction norm depends on the selectivity of mortality in terms of size and maturity state. Finally, for a given mortality regime, position and shape of the maturation reaction norm predictably vary with some key life history characteristics of the harvested species: the average somatic growth rate and the strength of the trade-off between growth and reproduction.

Appendices

Appendix A: Population Dynamics

The size s of an individual determines its life history stage. Given a growth trajectory (g_l, g_j), the size is itself determined by the age a, so that (a) the *larval stage* extends from birth to the age at metamorphosis, $0 \le a \le a_s(g_l)$, where $a_s(g_l) = s_s / g_l$, (b) the *juvenile stage* extends from the age at metamorphosis to the age at maturation, $a_s(g_l) < a \le a_m(g_l, g_j)$, where the latter is determined by the intersection between the maturation reaction norm S_m and the growth curve, and (c) the *adult stage* begins with maturation, $a > a_m(g_l, g_j)$.

The size $s(a, g_l, g_j)$ of an individual at age a and with growth trajectory (g_l, g_j) is given by $g_l a$ at larval stage, $\mathrm{s_s} + \mathrm{g_j} \cdot (\alpha - \alpha_\mathrm{s}(\mathrm{g_l}))$ at juvenile stage, and $s_m(g_l, g_j)$ $+\mathrm{g_a} \cdot (\alpha - \alpha_\mathrm{m}(\mathrm{g_l}, \mathrm{g_j}))$ at adult stage, with $\mathrm{g_a} = \mathrm{g_j} \cdot (1 - \Delta)$.

Only adults reproduce, and their fecundity or per capita birth rate b is proportional to the cube of body length, $\mathrm{b} = \alpha_\mathrm{b} \mathrm{s}^3$, with a scaling factor α_b.

The death rate $d(a, g_l, g_j, n)$ is given by $m_l(g_l)$ at larval stage, $m_j(g_j) + h(a, g_j, n)$ at juvenile stage, and $m_a(g_j) + h(a, g_j, n)$ at adult stage, where m is the natural density-independent mortality rate and $h(a, g_j, n)$ is the harvest mortality rate for an individual of age a living in an environment with growth rate g_j.

Then, the rate of change in the density n of individuals with age a and growth trajectory (g_l, g_j) is given by

$$\frac{\partial}{\partial t} n(a, g_l, g_j) = -\frac{\partial}{\partial a} n(a, g_l, g_j) - d(a, g_l, g_j, n) n(a, g_l, g_j),$$

with a boundary condition at age $a = 0$ and two continuity conditions at age $a = a_s$ and $a = a_m$, as follows. With $n(0)$ denoting the total number of larvae produced in the population,

$$n(0) = \iint \int_{a_m(g_l, g_j)}^{+\infty} b(a, g_l, g_j) n(a, g_l, g_j) \, \mathrm{d}a \, \mathrm{d}g_l \, \mathrm{d}g_j,$$

the boundary condition gives the number of larvae recruited at age 0 for each environmental trajectory (g_l, g_j), $\mathrm{n}(0, \mathrm{g_l}, \mathrm{g_j}) = \mathrm{k}(\mathrm{g_l}) \cdot \mathrm{o}(\mathrm{g_l}) \cdot \mathrm{o}(\mathrm{g_j}) \cdot \mathrm{n}(0) / (1 + \mathrm{n}(0))$ where $o(g_l)$ is the frequency of environments with growth rate g_l, and $k(g_l)$ is their larval carrying capacity. The first continuity condition gives the density of juveniles selecting habitats with growth rate g_j at age a_s, $n(a_s^+, g_l, g_j) = n(a_s^-, g_l, g_j) p(g_j)$ where p is the probability distribution describing habitat selection. The second continuity condition gives the density of adults at age a_m for each environmental trajectory (g_l, g_j), $n(a_m^+, g_l, g_j) = n(a_m^-, g_l, g_j)$.

The population dynamics just defined has no analytical solution. However, at equilibrium, i.e., when the rate of change in the density n is equal to 0, we can obtain the stable distribution n^* of individuals across ages a and growth trajectories (g_l, g_j),

$$n^*(a, g_l, g_j) = n^*(0, g_l, g_j)\exp(-d_l(g_l)a),$$

$$n^*(a, g_l, g_j) = n^*(a_s, g_l, g_j)\exp(-\int_{a_s(g_l)}^{a} d_j(a', g_j, n^*)\,\mathrm{d}a'), \text{ and}$$

$$n^*(a, g_l, g_j) = n^*(a_m, g_l, g_j)\exp(-\int_{a_m(g_l, g_j)}^{a} d_a(a', g_j, n^*)\,\mathrm{d}a')$$

for larval, juvenile, and adult stage, respectively.

Appendix B: Invasion Fitness

The invasion fitness, i.e., the long-term per capita growth rate of a rare mutant with reaction norm S'_m arising in a resident population with reaction norm S_m that has reached its population dynamical equilibrium $n^*(S_m)$, is extracted from the above population dynamics, which gives

$$f(S'_m, S_m) = \int\int\int [Kb(S'_m, a, g_l, g_j) - d(S'_m, a, g_l, g_j, n^*(S_m))] \cdot$$

$$n^*(S'_m, a, g_l, g_j)/\bar{n}^*(S'_m)\,\mathrm{d}a\,\mathrm{d}g_l\,\mathrm{d}g_j,$$

with $K = \int k(g_l)o(g_l)/(k(g_l) + n(0))\,\mathrm{d}g_l$ .This can be understood as follows. The long-term per capita growth rate is obtained as the sum over all ages a and growth trajectories (g_l, g_j) of the difference between the birth rate $b(S'_m, a, g_l, g_j)$, discounted by the density-dependent mortality of larvae, and the death rate $d(S'_m, a, g_l, g_j, n^*(S_m))$ of an individual, weighed by the probability distribution of individuals across ages and growth trajectories $n^*(S'_m, a, g_l, g_j)/\bar{n}^*(S'_m)$, where $\bar{n}^*(S'_m)$ is the total number of individuals in the population. Notice that for the derivation of invasion fitness the mutant density $n^*(S'_m)$ can be neglected in density-dependent processes because it is supposed rare when occurring. Notice also that, by definition, a resident individual has zero invasion fitness in its own population, $f(S_m, S_m) = 0$, since the long-term per capita growth rate is equal to 0 when the population is at its dynamical equilibrium.

Appendix C: Population Biomass

Assuming that the weight of individuals is proportional to the cube of their body length, the total biomass B of the harvested part of the population is

$$B(n^*) = \int \beta(g_j, n^*) o(g_j)\, \mathrm{d}g_j$$

$$= \alpha_w \int\int \int_{a_{\inf}}^{a_{\sup}} s^3(a, g_l, g_j) n^*(a, g_l, g_j)\, \mathrm{d}a\, \mathrm{d}g_l\, \mathrm{d}g_j ,$$

where α_w is a scaling factor and the integration boundaries $(a_{\inf}, a_{\sup})$ depend on harvesting practice. For state-dependent harvesting, they are equal to $(a_s(g_l), a_m(g_l, g_j))$ if juveniles are harvested, or to $(a_m(g_l, g_j), +\infty)$ if adults are harvested. For harvesting with a minimum size $s_{\min}$, the boundaries are $(a_{\min}(g_l, g_j), +\infty)$, with $a_{\min}(g_l, g_j)$ denoting the age at which an individual with environmental trajectory (g_l, g_j) reaches the minimum size $s_{\min}$. Of course harvest mortality rate $h(a, g_j, n^*)$ only applies to individuals for which $a_{\inf} \le a \le a_{\sup}$. Harvesting effort η in environment g_j is then given by

$$\eta(g_j, n^*) = \beta(g_j, n^*) / \int \beta(g_j, n^*)\, \mathrm{d}g_j .$$

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