Theme Session Y:

The effects of fishing on the genetic composition of living marine resources

Fisheries-Induced Changes in Age and Size at Maturation and Understanding the Potential for Selection-Induced Stock Collapse

Bruno Ernande[1], Ulf Dieckmann[1], and Mikko Heino[1,2]

[1]*Adaptive Dynamics Network, International Institute for Applied Systems Analysis,*

A-2361 Laxenburg, Austria

surname@iiasa.ac.at

[2]*Institute of Marine Research, P.O. Box 1870 Nordnes, N-5871 Bergen, Norway*

mikko.heino@imr.no

Abstract

Fishing is very likely to create selective pressures inducing adaptive changes in the life histories of harvested stocks. Using field data and adequate statistical methods, such alterations can be demonstrated. However, in order to understand underlying causes and to evaluate alternative management practices, past selective pressures must be quantified and predictions of future evolutionary changes are needed. In this respect, modelling the ecological and evolutionary dynamics of exploited stocks is a critical challenge. To illustrate this point, we studied the evolution of age and size at maturation induced by fishing using adaptive dynamics theory – a framework that allows modelling long-term evolution of quantitative traits under density- and frequency-dependent selection. Specifically, we investigated the evolutionary implications of alternative management policies. As a novel contribution to the discussion of fisheries-induced adaptive change, we showed that frequency-dependent selection, arising from fishing mortality under some particular management policies, can not only reduce the age and size at maturation and thus stock biomass, but can ultimately even induce the extinction of entire stocks. The potential for such phenomena of 'evolutionary suicide' is overlooked in models that do not incorporate life history evolution. Our findings thus highlight the importance of considering evolutionary trends in the management of exploited stocks.

Key words.—age and size at maturation; fisheries; adaptive changes; evolution; density dependence; frequency dependence; selective pressures; management rules; stock abundance; evolutionary suicide

1. Introduction

Fishing creates selective pressures that induce adaptive phenotypic changes in commercially exploited stocks (Trippel 1995; Rochet 1998; Law 2000). Such phenotypic changes could arise from two different mechanisms (Rijnsdorp 1992; Reznick 1993; Law 2000). The first mechanism is phenotypic plasticity. Fish have evolved highly plastic life histories (or, more generally, phenotypes) in face of their unpredictable environment. Here one can think of behavioral or physiological changes triggered by environmental parameters, like temperature or availability of food resources, but also of morphological characters, like the change in body shape in response to the presence of predators (Brönmark and Miner 1992; Brönmark *et al.* 1995; Holopainen *et al.* 1997) or some polymorphism in the shape of the feeding apparatus due to heterogeneity in trophic resources (Day and McPhail 1996). Such phenotypic plasticity allows fish to react to environmental changes by modifying their phenotype in the short term (a single genotype potentially giving rise to different phenotypes), and more specifically, to plastically adapt to the fisheries-induced alterations of environmental conditions. The second possible fisheries-induced adaptive response would consist of evolutionary changes in the life histories of harvested stocks, manifesting some underlying modifications in their genetic composition. Indeed, fisheries are bound to alter the genetic composition of exploited stocks by removing some individuals in preference to others (according to size for instance). This may result in rapid and abrupt evolutionary changes.

Management implications of genetic and phenotypically plastic changes are quite different: mitigating adverse genetic changes takes generations, whereas phenotypically plastic responses occur within generations. For management purposes, therefore, one has to distinguish between these two possible kinds of adaptive changes. Phenotypic plasticity can be depicted by reaction norms, which themselves are genetically determined traits. Indeed, every genotype is theoretically characterized by a specific reaction norm, the set of phenotypes that a genotype would plastically express across a given range of environments (Schmalhausen 1949). Therefore, if there is any chance for phenotypic plasticity to be involved, evolutionary (or genetic) changes in exploited fish stocks should be assessed in terms of reaction norms. By contrast, a mere displacement of expressed phenotypes along the reaction norm leaves the reaction norm itself unchanged.

The application of adequate statistical methods on field data allows testing for evolutionary modifications in reaction norms (Heino *et al.* 2002a, b) and thus assessing genetic changes in harvested stocks. However, once such change has been demonstrated, we need to identify the

responsible selective pressures in order to evaluate potential changes in management. Modelling the evolution of reaction norms then becomes indispensable: it allows identifying past selective pressures (natural and fisheries-induced) that were responsible for the observed adaptive changes, and it permits predicting future changes based on current selective pressures.

This paper illustrates the possible use of theoretical tools for management purpose by a model for the evolutionary dynamics of reaction norms of age and size at maturation in exploited fish stocks. Age and size at maturation are important life history traits since they influence the probability to survive until maturity, the subsequent reproductive effort and growth, 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 fish biology and fisheries. Generally, fishing mortality strongly depends on size or maturity status and is thus expected to result in adaptive changes in growth and maturation. Knowing that age and size at maturation affect the age and size composition of fish stocks and thereby their reproductive potential (Marshall *et al.* 1998), any change in those traits might indeed have strong repercussions on stock dynamics (Stergiou 2002).

2. A Short Introduction to Adaptive Dynamics Theory

We introduce here the theory of adaptive dynamics (Metz *et al.* 1992; Dieckmann 1994; Dieckmann and Law 1996; Metz *et al.* 1996; Geritz *et al.* 1997; Geritz *et al.* 1998) that we use to model the evolutionary dynamics of maturation reaction norms. At the expense of genetic details, this theoretical framework allows to consider the long-term evolution of phenotypic traits such as reaction norms, to derive selective pressures from explicit ecological scenarios, and to describe evolutionary dynamics as well as evolutionary equilibria. Most importantly, adaptive dynamics models can account for any types of density- and frequency-dependent selection pressures, i.e. that depend on the other phenotypes present in the population. Indeed, when considering ecological interactions, like competition for resources, predation, or harvesting, from the perspective of an individual, the conspecific individuals are part of the environment and are then involved in the selective pressures acting on that individual. This is frequency-dependent selection (Metz *et al.* 1992; Metz *et al.* 1996; Heino *et al.* 1998; Meszéna *et al.* 2002), a common feature in nature that has been encompassed as a generic case in the adaptive dynamics theory.

Adaptive dynamics analysis is based on the translation of natural selection into invasion processes. One considers a resident population with a given phenotypic composition $p_1, p_2, p_3, ...$ and predicts whether a mutant, i.e. an individual with a new phenotype p' arising in that population, survives and spreads in the resident population or dies — this is readily 'selection of the fittest'. Long-term evolutionary dynamics can then be modelled as successions of invasion events in the course of which resident populations are replaced by advantageous mutants, which results in sequences of phenotypic substitution in the population i.e. phenotypic evolutionary dynamics.

Predicting whether a mutant can invade or not is therefore critical in adaptive dynamics analysis and one needs an invasion criterion, which is given by the invasion fitness of the mutants. The invasion fitness of a rare mutant p' is defined as the expected long-term per capita growth rate of that mutant in an environment set by the resident population $p_1, p_2, p_3, ...$ that has reached its population dynamical equilibrium (Metz *et al.* 1992; Rand *et al.* 1994; Ferrière and Gatto 1995).

Under some specific conditions, a monomorphic deterministic approximation of the sequences of phenotypic substitutions can be obtained. Evolutionary trajectories of phenotypes are then described by an ordinary differential equation, the so-called canonical equation of adaptive dynamics (Dieckmann 1994; Dieckmann and Law 1996; Dieckmann *et al.* in preparation), which mainly depends on the selection gradient that is itself obtained as the derivative of the invasion fitness according to the evolving trait.

Then, typical adaptive dynamics analysis proceeds through four successive steps:

■ *Step 1: Population dynamics*. Construct a model of population dynamics based on the life history of interest and including all relevant ecological features, especially individual interactions giving rise to density- and frequency-dependence.

■ *Step 2: Invasion fitness*. Extract from the population dynamics the invasion fitness by computing the long-term per capita growth rate of a rare mutant arising in a resident population that has reached its population dynamical attractor.

■ *Step 3: Selection gradient*. Derive the selection gradient from the invasion fitness.

■ *Step 4: Evolutionary dynamics*. Introduce the selection gradient in the canonical equation to observe the evolutionary transient states as well as the resulting evolutionary equilibria.

In the following, we apply this type of analysis to investigate the evolution of maturation reaction norms in exploited fish stocks. Specifically, we consider a fish stock that experiences a heterogeneous environment leading to plasticity of age and size at maturation. We represent

plastic variation in age and size at maturation by a reaction norm $S_m(a_m)$. Then, we focus on the evolutionary dynamics of this reaction norm under fishing pressure and the possible repercussions of these dynamics on stock abundance for three alternative management policies.

3. Stock Life History and Population Dynamics Model

We describe here the main characteristics of the population dynamics model used in this paper (mathematical details will be published elsewhere).

We consider a population model that mimics the life cycle of a coastal fish species (Figure 1a). The life cycle is divided into three stages – larvae (l), juveniles (j), and adults (a), connected by three transitions – metamorphosis, maturation and reproduction. The fish distribute differently along a heterogeneous coastal environment, depending on their stage. First, larvae are distributed at random across the environments because their limited swimming capacity precludes habitat selection. After metamorphosis individuals gain better swimming capability such that they can actively select their habitat. We assume here that habitat choice is made only once, just after metamorphosis, and that fish settle to this habitat for the remainder of their life. Individual fish thus experience an environmental trajectory (e_l, e_{ja}) consisting of their larval and juvenile-adult environment (path indicated by the thick arrows in Figure 1a).

Death rates depend on life history stage of fish. Mortality in the larval stage is dramatically higher than later in life, and high larval densities can lead to intense resource competition (Wootton 1998). We assume that larvae compete only with each other (and not with juveniles and adults which are assumed to have different diets), such that population regulation takes place during the larval stage. The larval death rate d_l is thus given by a density-independent mortality rate m_l plus a logistically density-dependent component with carrying capacity k. By contrast, juvenile and adult death rates are assumed to be density-independent, $d_j = m_j$ and $d_a = m_a$.

Somatic growth is affected by the transitions between stages (Figure 1b). We suppose that length growth is linear with age and that growth rates, g_l, g_j, and g_a, differ between stages. Larvae metamorphose into juveniles when they reach a fixed size threshold, s_s. By contrast,
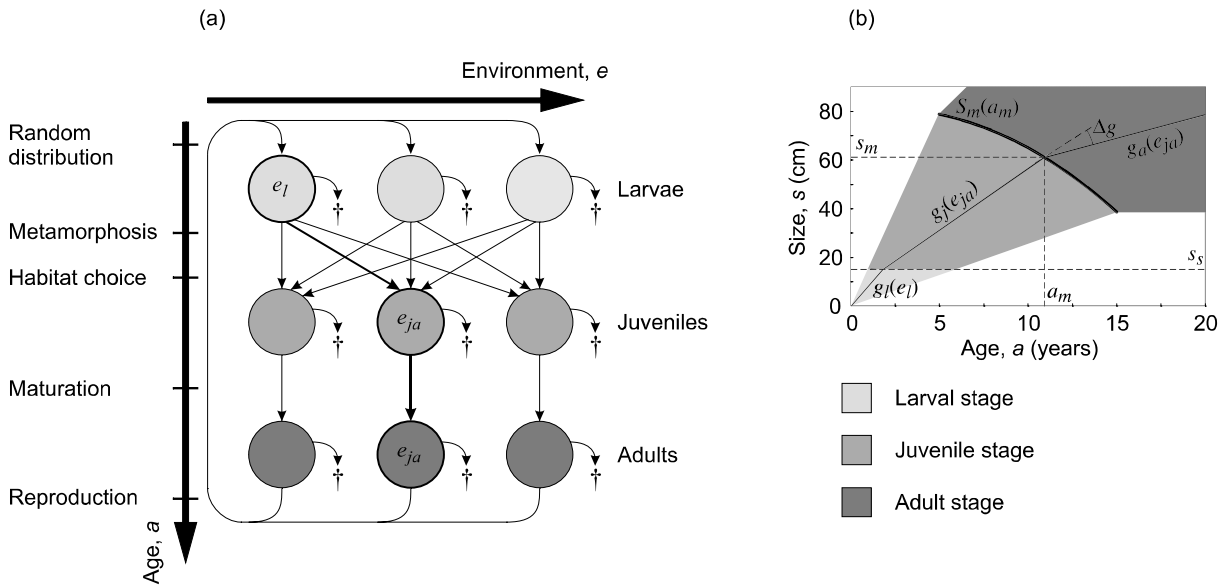
Figure 1. Stock life history. (a) Life cycle and environmental heterogeneity. We consider a stage- and age-structured population that experiences a heterogeneous environment. Fish pass through three life-history stages, larva, juvenile, and adult, and experience three life-history transitions, metamorphosis, maturation, and reproduction. The black thick path illustrates the life history of a single individual. (b) Somatic growth and its dependence on metamorphosis and maturation. 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 variability. Metamorphosis and maturation are fully determined by somatic growth. Fish metamorphose from larva to juvenile when their growth trajectory (thin black 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 black curve). Due to environmental heterogeneity, fish metamorphose at different ages (but at fixed size s_s) and mature at different ages and sizes (a_m, s_m).

age a_m and size s_m at maturation are plastic, and the reaction norm $S_m(a_m)$ describes their variation. Maturation occurs when the growth trajectory intersects with the reaction norm. In addition, after maturation individuals face an energy allocation trade-off between reproduction and somatic growth; this is captured by considering a reduced growth rate for mature fish, $g_a = g_j - \Delta g$ (setting Δg constant with respect to body length is an acceptable assumption as soon as the gonado-somatic index is not too large). Finally, the fecundity of mature fishes strongly depends on size (Roff 1984, 1992; Wootton 1998); we assume that per capita fecundity is proportional to the cube of body size.

Environmental heterogeneity results in larval carrying capacities $k(e)$ and growth rates $g_l(e)$, $g_j(e)$, $g_a(e)$, to vary with environment e. Assuming a certain maturation reaction norm (see below), each fish is then characterized by three state variables: its age a and its environmental trajectory (e_l, e_{ja}). Somatic growth being deterministic, size and thus stage and fecundity are fully determined by these state variables. A continuous-time structured population model accounting for the three state variables (a, e_l, e_{ja}) therefore describes the population dynamics (details not given).

4. Evolution of Maturation Reaction Norms Without Fishing

Based on the population dynamics model and following the four steps of adaptive dynamics analysis, we obtain the canonical equation for the evolutionary dynamics of the maturation reaction norm S_m. Throughout the rest of the analysis, we focus on the evolutionary trajectories of S_m and the evolutionary equilibria S_m^*; these equilibria represent the end points of evolution where no further change occurs.

 We start our study by assessing the evolution of maturation reaction norms in the absence of harvesting. In this scenario, death rates are only determined by natural mortality. Figure 2 displays the end points of reaction norm evolution for different ratios m_j / m_a between juvenile and adult mortality rates. An increase in this ratio has two simultaneous effects: the reaction norm is displaced toward lower ages and sizes, and, in addition, its slope changes from negative to positive. Notice that we find no case where maturation is determined only by age (vertical reaction norm), and maturation at fixed size (horizontal reaction norm) only appears as an intermediate case.
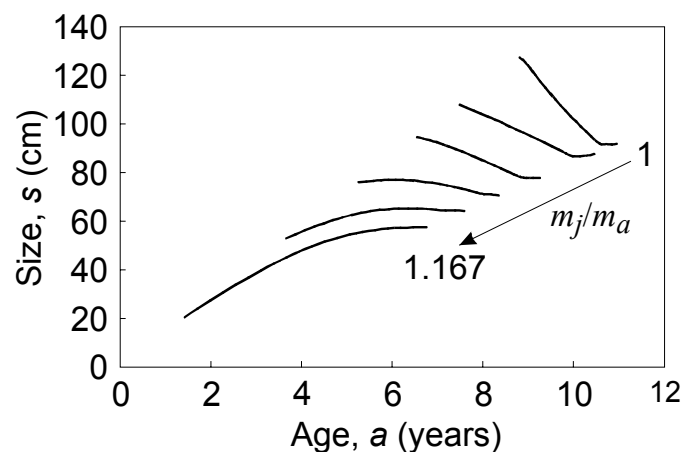

Figure 2. Outcomes of maturation reaction norm evolution in the absence of harvesting. Somatic growth rates are given by $g_l(e)$ = 15-7.e and $g_a(e)$ = $g_l(e)$-Δg, with e scaled to the interval [0, 1] and Δg = 2. The different end point reaction norms are obtained for different ratios m_j / m_a between juvenile and adult mortality rates with m_a fixed to 0.15 and m_j varying from 0.15 to 0.175 with step size 0.005. Increasing this ratio displaces the reaction norm to lower ages and sizes at maturation and changes the reaction norm slope from negative to positive.

5. Fisheries-Induced Evolution of Maturation Reaction Norms

5.1. Harvesting and management policies

We now concentrate on the effect of harvesting on evolving reaction norms for maturation. Harvesting may only affect juveniles and/or adults, so that fishing mortality adds to the density-independent natural mortality rates experienced by these two stages. Three management strategies can be considered (e.g. Hilborn and Walters 1992):

- *Fixed quotas*: the total biomass γ of the fish in catch is fixed. This rule leads to a fishing mortality $H(B) = \gamma / B$ which decreases with total stock biomass B and thus is positively density-dependent (Figure 3, curve FQ).

- *Constant harvesting rate*: a fixed proportion ρ of the total stock biomass is caught. This rule gives density-independent fishing mortality $H = \rho$ (Figure 3, curve CHR).

- *Constant stock size*: the stock biomass after harvesting κ is kept constant. This rule leads to negatively density-dependent fishing mortality $H(B) = 1 - \kappa / B$ (Figure 3, curve CSS).
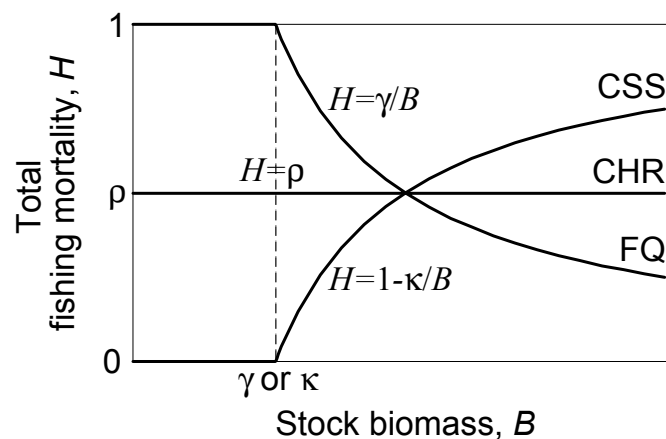

Figure 3. Variation of total fishing mortality with stock biomass for three alternative management rules. Whether or not total fishing mortality *H* depends on total stock biomass *B* depends on the management rule applied. For Fixed Quotas (curve FQ), the total caught biomass is fixed to an amount *γ* and the total fishing mortality decreases with stock biomass *B*, resulting in positive density dependence. For Constant Harvesting Rate (curve CHR), the proportion *ρ* of the stock biomass that is caught is fixed and the resulting fishing mortality is density-independent. For Constant Stock Size (curve CSS), the stock biomass after harvesting is fixed to an amount *κ* and the total fishing mortality increases with stock biomass *B*, resulting in negative density dependence.

While the management policy determines fishing mortality at the level of the whole stock $H(B)$, the distribution of harvesting effort may still be heterogeneous across environments and result in variations in local fishing mortality. In particular, fishermen are likely to focus their effort on environments where fish are abundant. Therefore, we assume harvesting effort η in environment e to be proportional to local stock biomass $b(e)$, $\eta(e) = b(e) / B$ with

$\int \eta(e)\,de = 1$. Then the local fishing mortality in environment e is equal to $\eta(e)H(B)$ (Figure 4).
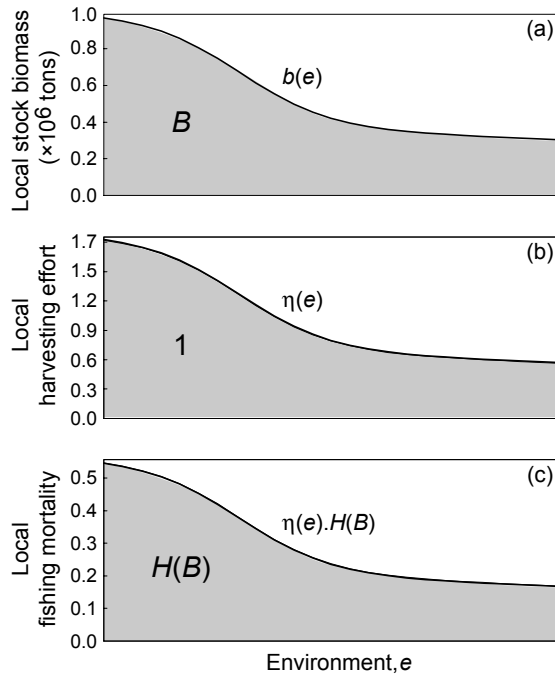

Figure 4. Fishing mortality and its relationship with stock biomass. Panel (a) presents a hypothetic distribution of local stock biomass $b(e)$ across environments e. The area under the curve is then the total stock biomass,

$$B = \int b(e)\,de\,.$$

Panel (b) shows how local harvesting effort $\eta(e)$ varies across environments according to local stock biomass. Fisheries concentrate on environments where fish are abundant. As $\eta(e)$ is a frequency distribution, the area under its curve is equal to 1,

$$\int \eta(e)\,de = \int \frac{b(e)}{B}\,de = 1\,.$$

Multiplying local harvesting effort by total fishing mortality $H(B)$, determined according to the management rules described in the main text, gives local fishing mortality as shown in panel (c). The area under the curve is then the total fishing mortality,

$$H(B) = \int \eta(e).H(B)\,de = \int \frac{b(e)}{B}.H(B)\,de\,.$$

Notice that the variation of death rates across environments stems from differential harvesting efforts and that harvesting implies two levels of density dependence: density dependence at the level of the whole stock that can affect the total fishing mortality $H(B)$, and local density dependence that influences the harvesting effort $\eta(e)$ in a given environment. Therefore, whatever the management strategy is, harvesting is density-dependent and, thus, can induce frequency-dependent selection.

5.2. Effects of status-dependent harvesting on the evolution of maturation reaction norm

We first focus on the two cases in which either only immature or only mature fishes are caught and refer to these as cases of status-dependent harvesting. This readily occurs when nursery and spawning grounds are segregated and fishermen target concentrations of fish in these specific habitats. In this case, the target stock is either the juvenile or the adult part of stock, and the biomass is computed accordingly (details not given). It is clear then that status-dependent harvesting modifies the ratio between juvenile and adult death rates, which, according to the previous section, must be expected to have great repercussions for the resultant maturation reaction norm.

Figure 5 shows the effect of increasing harvesting pressure on adults for the three management rules. The observed effect is the same for the three management rules and could already have been predicted from the preceding. As harvesting of spawning fish increases, the reaction norm is displaced toward higher ages and sizes and its slope changes from positive to negative. Two small differences from case without harvesting can be noticed. First, the displacement of the reaction norm is smaller and, second, some cases of maturation at fixed age (vertical reaction norm) can appear when fishing mortality on adults is sufficiently high.
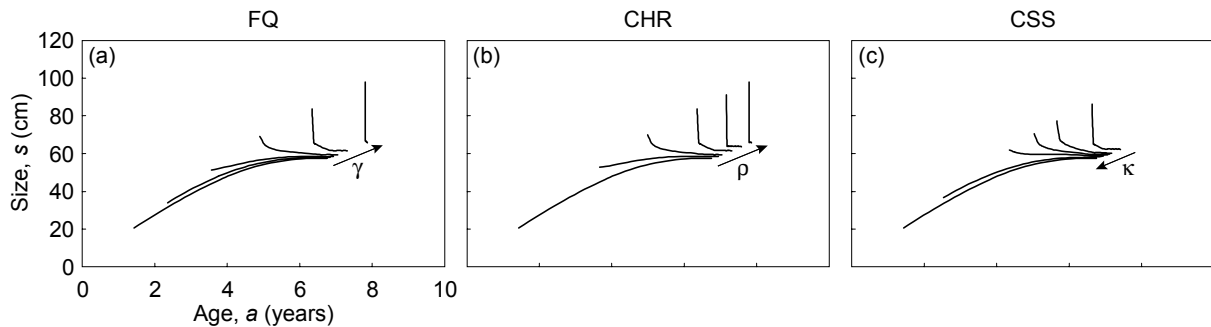

Figure 5. Outcomes of reaction norm evolution under status-dependent harvesting. In this example, we consider that fishing focuses only on the adult stock. The juvenile and adult death rates are given as $d_j(e_{ja}) = m_j$ and $d_a(e_{ja}) = m_j + \eta(e_{ja}).H(B)$ with $m_j = 0.175$ and $m_a = 0.15$, such that $m_j / m_a = 1.167$, and growth rates vary across environments as described in Figure 2. Panels (a), (b) and (c) present the effect of increasing harvesting pressure for Fixed Quotas, Constant Harvesting Rate, and Constant Stock Size rules, respectively. Quotas γ increase from 0 to 10^8, i.e., from 0% to 1.9% of the unharvested stock biomass, with step size 2×10^7, harvesting rate ρ increases from 0 to 0.02 with step size 0.004, and fixed stock size κ decreases from 5.4×10^9 to 4.9×10^9, i.e. from 100% to 90.7% of the unharvested stock biomass, with step size 10^8.

5.3. Effects of harvesting with size limit on the evolution of maturation reaction norm

We investigate a management policy that prescribes a minimum landing size s_{min} irrespective of maturation status (Hilborn and Walters 1992). In this case, the target stock consists of all fish larger than s_{min}, leading to size-dependent harvesting. The position of the maturation reaction norm relative to the minimum landing size dictates whether fishing mortality mostly affects juveniles or adults.

Figure 6 depicts the effect of increasing the minimum landing size and the harvesting pressure for the three management rules. Once more, the effects are qualitatively the same for the three management rules. Increasing the harvesting pressure displaces the reaction norm toward lower ages and sizes but contrary to the previous case, has almost no effect on its slope. Increasing the minimum landing size while keeping the same harvesting pressures has a more subtle effect. Reaction norms that are initially below the minimum landing size move toward higher sizes and ages, whereas the reverse applies to those lying above. Reaction
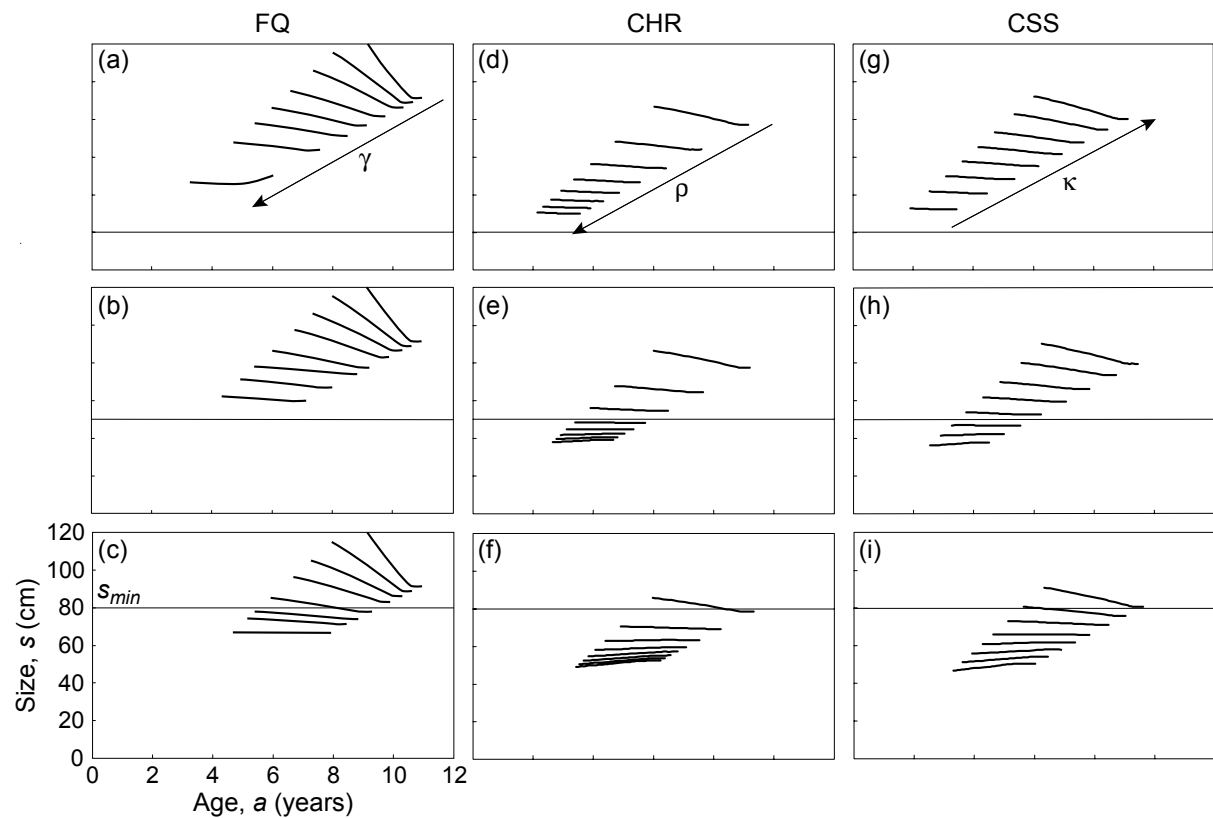
Figure 6. Outcomes of reaction norm evolution under harvesting with size-limit. In this example, stock management policy prescribes a minimum landing size s_{min}, so that only fishes larger than s_{min} are harvested. The ratio between juvenile and adult density-independent mortality rates is set to $m_j / m_a = 1$ ($m_j = m_a = 0.15$) and growth rates vary across environments as described in Figure 2. We consider three possible landing sizes $s_{min} = 20$ cm, 50 cm, and 80 cm. The effect of increasing the harvesting pressure for these three minimum landing sizes is presented for Fixed Quotas in panels (a), (b), and (c), for Constant Harvesting Rate in panels (d), (e), and (f), and for Constant Stock Size rule in panels (g), (h), and (i). Quotas γ vary from 0 to 3.5×10^9, i.e., from 0% to 6.7% of the unharvested stock biomass, with step size 5×10^8, harvesting rate ρ increases from 0.05 to 0.4 with step size 0.05, and fixed stock sizes κ decreases from 4.5×10^{10} to 10^{10}, i.e., from 73.5% to 16.5% of the unharvested stock biomass, with step size 5×10^9.

norms thus tend to evolve toward the minimum landing size s_{min}. This effect is explained by the position of the initial reaction norm relative to the minimum landing size. If the reaction norm initially lies below s_{min}, only mature fishes are harvested. Thereby, the ratio between juvenile and adult death rates decreases and, as seen before, the reaction norm is displaced toward higher ages and sizes. Conversely, if the reaction norm initially lies above s_{min}, both immature and mature individuals are fished, which results in earlier ages and smaller sizes at maturation.

5.4. The danger of selection-induced stock collapse

To conclude our analysis, we highlight the potential consequences of maturation reaction norm evolution for stock biomass and density. We again consider a minimum landing size

s_{min} (fixed to 20 cm) and the Fixed Quotas rule (with the quota γ fixed to a value corresponding to a mere 6.7% of the virgin stock biomass).

The resulting evolutionary trajectory of maturation reaction norms and its effect on stock biomass and density are depicted in Figure 7. As seen in the previous example, the reaction norm for maturation evolves toward lower ages and sizes, because it initially lies above the minimum landing size (Figure 7a). As a result of this evolutionary trajectory, the trade-off between somatic growth and fecundity is expressed at progressively earlier age, and stock biomass decreases accordingly (Figure 7b). As a simultaneous effect, the total fecundity in the stock declines because of the smaller size of mature individuals, leading to a decrease in stock density (Figure 7c). Finally, the Fixed Quotas rule leads to an increase in fishing mortality due to positive density dependence (Figure 7d). Consequently, the reaction norm evolves toward even lower ages and sizes, until, eventually, the stock collapses.
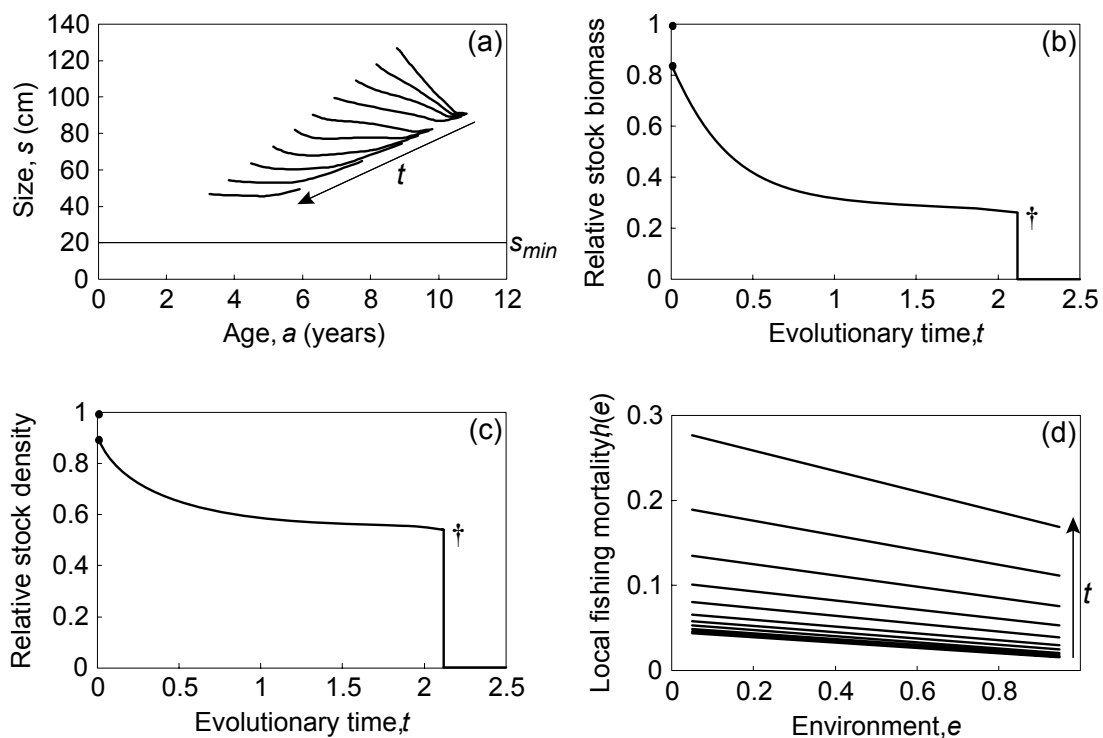

Figure 7. Fisheries-induced stock collapse through natural selection. In this example, we consider the same situation as in Figure 6a with s_{min} fixed to 20 cm and γ fixed to 3.5×10^9, i.e., 6.7% of the unharvested stock biomass. Panel (a) presents the evolutionary trajectory of the maturation reaction norm. Panel (b) depicts changes in stock biomass over evolutionary time. For greater clarity, stock biomass is shown in relative units, with a value of 1 corresponding to the unharvested stock biomass. The initial point of the curve thus shows the population dynamical consequences of harvesting on the stock, without taking into account the subsequent evolutionary changes, which are depicted by the curve itself. Panel (c) presents the changes in local fishing mortality across environments over evolutionary time. Panel (d) shows how stock density changes over evolutionary time. As in the case of biomass, stock density is shown in relative units. Notice that the eventual stock collapse is not foreshadowed by a precipitous decline in either stock biomass or stock density, making it particularly perfidious from a management point of view.

Such population extinction driven by natural selection is called evolutionary suicide (Matsuda and Abrams 1994; Ferrière 2000; Gyllenberg *et al.* 2002; Ferrière and Dieckmann in press; Parvinen and Dieckmann in press) and occurs most readily under frequency-dependent selection. Evolutionary models that do not include frequency-dependent selection (like most traditional reaction norm models) would overlook it. In the same way, a simple population dynamics model would predict sustainability of the stock. In fact, a simple population dynamics model predict a decrease of only 18% for the stock biomass and 10% for the stock density, relative to the unharvested stock, as shown by the initial, isolated point of the curves in Figures 7b and 7c. A very simple way to avoid stock extinction is this particular example is to increase the minimum landing size s_{min}. Indeed, for $s_{min} = 50\,\text{cm}$, for example, no evolutionary suicide is observed in the model, whatever the harvesting pressure (not illustrated).

6. Conclusion

Using adaptive dynamics theory, this paper investigates potential evolutionary changes induced by harvesting on fish stocks. We have shown in some detail how harvesting is a selective pressure that can shape and displace the reaction norm for age and size at maturation. Specifically, the position of the maturation reaction norm is predicted to change according to the life history stage that is harvested. Harvesting on mature individuals should induce later ages and larger sizes at maturation, whereas harvesting on immature fish would displace the reaction norm toward lower ages and sizes. The shape of the maturation reaction norm is also predicted to evolve under harvesting pressure. Indeed, the ratio between immature and mature death rates, which can be altered by fishing mortality, appears to be particularly critical for determining the global slope of the reaction norm.

Some limitations of our approach, however, have to be noticed. Firstly, genetic details were neglected 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 out of consideration. Second, in order to simplify the analysis, some particular aspects of fish biology were overlooked. Most importantly, we have ignored density-dependent somatic growth (Lorenzen and Enberg 2002), which could change, at least quantitatively, the evolution of the maturation reaction norm.

One important feature of the presented model is that it allows for any reaction norm shape to evolve. In this respect, it is important to notice that the simplifying assumption of fixed-age or fixed-size at maturation used in some life history evolution models is not supported. Indeed, vertical (fixed-age) or flat (fixed-size) maturation reaction norms only appeared as intermediate or specific cases and, generally, predicted reaction norms for maturation allow for both age and size to vary.

The second important feature of our approach is that it allows considering the ecological repercussions of evolutionary changes. Two major ecological consequences of fisheries-induced evolutionary changes in the reaction norm for maturation became evident. First, if the reaction norm for maturation is displaced toward lower ages and sizes, this results in a decrease of the stock biomass because the trade-off between growth and reproduction is then expressed earlier. Second, harvesting can induce frequency-dependent selection, which may lead to self-extinction by natural selection. Simple population dynamics models would overlook such an effect since they do not account for the evolution of life history traits under harvesting; also evolutionary models that do not encompass frequency-dependent selection would not be able to predict the stock collapse. This highlights the importance of models as those developed here for the long-term management of living marine resources: considering evolutionary trends in exploited stocks should become a standard practice of responsible stock management.

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