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Management of evolving fish stocks

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IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 17

The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems

Focusing on these long-term implications of adaptive processes in systems of limited growth, the Adaptive Dynamics Network brings together scientists and institutions from around the world with IIASA acting as the central node.

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THE ADAPTIVE DYNAMICS NETWORK

The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

These and many more problems possess a common source: the interactions of individuals are bound to change the environments these individuals live in. By closing the feedback loop in the evolutionary explanation, a new mathematical theory of the evolution of complex adaptive systems arises. It is this general theoretical option that lies at the core of the emerging field of adaptive dynamics. In consequence a major promise of adaptive dynamics studies is to elucidate the long-term effects of the interactions between ecological and evolutionary processes.

A commitment to interfacing the theory with empirical applications is necessary both for validation and for management problems. For example, empirical evidence indicates that to control pests and diseases or to achieve sustainable harvesting of renewable resources evolutionary deliberation is already crucial on the time scale of two decades.

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Summary

Mortality caused by harvesting can select for life history changes in the harvested stock. Should this possibility be taken into account in the management of renewable resources? I compare the performance of different harvest strategies when evolutionary change is accounted for with the help of an age-structured population dynamics model. Assuming that age of first reproduction is the only evolving trait, harvesting of only mature individuals selects for delayed maturation and results in increased sustainable yields. Unselective harvesting of both mature and immature fish selects for earlier maturation which causes the sustainable yield to decrease. Constant stock size and constant harvest rate strategies perform equally well in terms of maximum sustainable yield, both before and after evolutionary change. The maximum sustainable yield for fixed quota strategies is lower. All those strategies have similar evolutionary consequences given a similar average harvest rate. Coevolutionary dynamics between fish stock and the stock manager indicate that the evolutionary benefits of selective harvesting are attainable without incurring yield losses in the near future.

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Management of evolving fish stocks

Mikko Heino

Introduction

Open access resources tend to be overexploited (Hardin 1968; Clark 1990), and management actions are usually necessary in order to achieve sustainable use of renewable resources. Harvest strategies are management tools which help to decide how the annual catches from a fish stock should be adjusted in response to stock size, to achieve sustainability and other objectives set by the management (Hilborn and Walters 1992). Harvest strategies have to cope with fluctuations in the stock size (whether these are caused by natural factors or are a consequence of harvesting itself) and with inherent inaccuracy of the estimates of stock size (Ludwig et al. 1993; Walters and Maguire 1996). Furthermore, harvest strategies must take into account economical, political and social consequences (Hilborn and Walters 1992).

In harvested fish stocks, the mortality caused by fishing often exceeds the mortality caused by natural factors (Pitcher and Hart 1982; Law and Grey 1989). As the mortality regime is known to be very important for age schedules of growth and reproduction (Roff 1992; Stearns 1992), fishing might be one of the major environmental factors inducing evolutionary change in exploited populations. This adds a new dimension to the management of fish stocks: should the possibility of evolutionary change, induced by the fishing mortality, be considered when setting management objectives? If yes, how do existing harvest strategies need to be changed? How are different harvest strategies performing before and after such evolutionary change? Although the problem has been acknowledged since the 70's at least (Borisov 1978) and has found its way even into some basic text books (Pitcher and Hart 1982; Wootton 1990; Bell 1997), scientific attempts towards analyzing the problem in more detail have been rather sporadic. Notable theoretical work include Law and Grey (1989), the papers in the volume edited by Stokes et al. (1993) and Kaitala and Getz (1995). Case studies analyzing real fish stocks include Rijnsdorp (1992, 1993). Healey (1978, 1980) reports on experimental work at the ecosystem scale.

This paper attempts to extend the pioneering work by Law and Grey (1989). These authors compared the performance of different age-specific harvest strategies after evolutionary change in fish, induced by a given harvest strategy, has taken place. They introduced the concept of the 'evolutionarily stable optimal harvesting strategy' (ESOHS), which is the strategy that maximizes yield *after* evolutionary change, neglecting possible short-term losses in yield it might incur. However, since Law and Grey (1989) studied harvesting only under steady state conditions, there was no possibility for assessing the performance and evolutionary consequences of different types of harvest strategies. A further complication is that if an ESOHS implies losses in yield in the near future, it is an acceptable management goal only if zero economic discount rates are assumed. Therefore, it is an important question whether ESOHS can be attained by optimizing harvest strategies to current fish life histories, without consideration of possible future gains or losses in yield due to evolutionary change.

Conceptual background

Optimal strategies are analysed here from two different perspectives, from that of a manager and from that of fish. Optimal strategies of the manager are based on rational decision making. Fish can attain optimal life history strategies by evolutionary change. Optimal strategies for the manager and for the fish generally depend on each other, leading to frequency dependence and coevolutionary dynamics.

Optimal harvest strategies

An optimal harvest strategy is the harvest strategy that best meets the objectives of management. One of the most simple objectives is the maximum sustainable yield (MSY) — the highest possible long-term average yield. While the MSY is theoretically well defined and also biologically justified objective, it is notoriously difficult to implement in practice (e.g. Hilborn and Walters 1992). Moreover, the objectives for real fisheries management are often multiple and take into account social and economic factors as well. Nevertheless, in the realm of models considerable insight to behaviour and performance of different harvest strategies can be achieved with the MSY as an objective. I will also use two other measures, namely the variability of annual catch and the average size of fish in the catch, for comparing different strategies.

Here I study three classes of harvest strategies in which the annual harvest depends only on the size of the stock. In fixed quota strategies, the annual target catch is fixed. In constant stock size strategies, the target stock size after harvesting is kept constant. In constant harvest rate strategies, a constant fraction of stock is harvested each year. The constant harvest rate strategies are commonly used for managing the commercially important fish stocks (Hilborn and Walters 1992). Within a class of harvest strategies, the varying parameters are annual quota (for fixed quota strategies), harvest rate (for constant harvest rate strategies) or target population size (for constant harvest rate strategies).

Conventionally, an optimal harvest strategy maximizes sustainable yield (or some other objective function), taking the life history characteristics of the fish as given. A manager sticking to such harvest strategies is an 'ecologically enlightened manager' of Brown and Parman (1993). Alternatively, the manager may anticipate that the fish evolve in response to harvesting. Such 'evolutionarily enlightened manager' (Brown and Parman 1993) chooses a harvest strategy that maximizes sustainable yield after evolutionary change has taken place and the fish has attained an ESS under that harvest regime. This harvest strategy is an ESOHS (Law and Grey 1989).

Evolutionarily optimal life history strategies

A life history strategy can be evolutionarily 'optimal' only in the sense that by adopting a different life history strategy no individual can do better, i.e. the strategy is uninvadable. Such strategy is called an evolutionarily stable strategy (ESS). To be a useful concept the ESS must also be convergent stable (see e.g. Eshel 1996). The crucial question is what is meant by 'doing better'. The new field of adaptive dynamics suggests that fitness should be measured in a population dynamical context (Dieckmann 1997). Populations do not only experience influence *from* the environment, but their actions also have influence *on* the environment. In the literature, the part of the environment which is influenced by the population is called feedback environment (Mylius and Diekmann 1995; Heino et al. 1997). The interaction between a population and its (feedback) environment assures that the population is neither growing nor decreasing in numbers in the long run. Mutant strategies experience the feedback environment as set by the resident population. If there is a strategy that sets the feedback environment such that no other strategy can increase in numbers, then that strategy is an ESS. The formalization of this idea leads to the concept of invasion fitness. In applying the invasion fitness concept, the basic tool is the so-called invasion exponent $\rho(\sigma, \mathbf{E})$ (mathematically the dominant Lyapunov exponent), which is the long-term average growth rate of a mutant playing strategy σ, growing in a feedback environment $\mathbf{E}$ set by the resident strategy (Metz et al. 1992; Rand et al. 1994; Ferrière and Gatto 1995). The evolutionarily optimal life history can then be identified as the strategy for which $\rho(\sigma, \mathbf{E}_{\sigma^*}) < 0$ for all $\sigma \neq \sigma^*$. In many models this condition can be evaluated only with the help of simulations. The G-function approach of Brown and Vincent (1987) is based on similar invasion criteria as presented above.

It is also possible that there is no single strategy that is uninvadable as a population strategy. Instead, two or more strategies may coexist, in a such way that they form a coalition which is able to resist invasions by all other types (Brown and Vincent 1987; Metz et al. 1996b; Geritz et al. 1998). Such strategies can be identified by mutual invasibility. A single strategy can give rise to a polymorphism of two strategies via an evolutionary branching. This option is not accounted for in the traditional evolutionary game theory.

Coevolutionary dynamics

A further complication is that change in fish life history may cause change in optimal harvest strategies, which in turn might induce further evolutionary change in the fish. This scenario probably reflects the situation attainable in real fisheries: the ecologically enlightened manager tracks the changes in fish without a consideration of the possible further evolutionary changes. With a slight misuse of the concept, I call this coevolutionary dynamics — here only the fish life history is evolving in the usual biological sense of the word. Nevertheless, it is clearly inappropriate to analyze optimal strategies of fish and of the manager in isolation. Coevolutionary dynamics may lead to an evolutionary resting point where it does not pay for either fish or the manager to depart from the prevailing strategies. However, more complicated outcomes are also possible: the coevolutionary change may continue indefinitely,

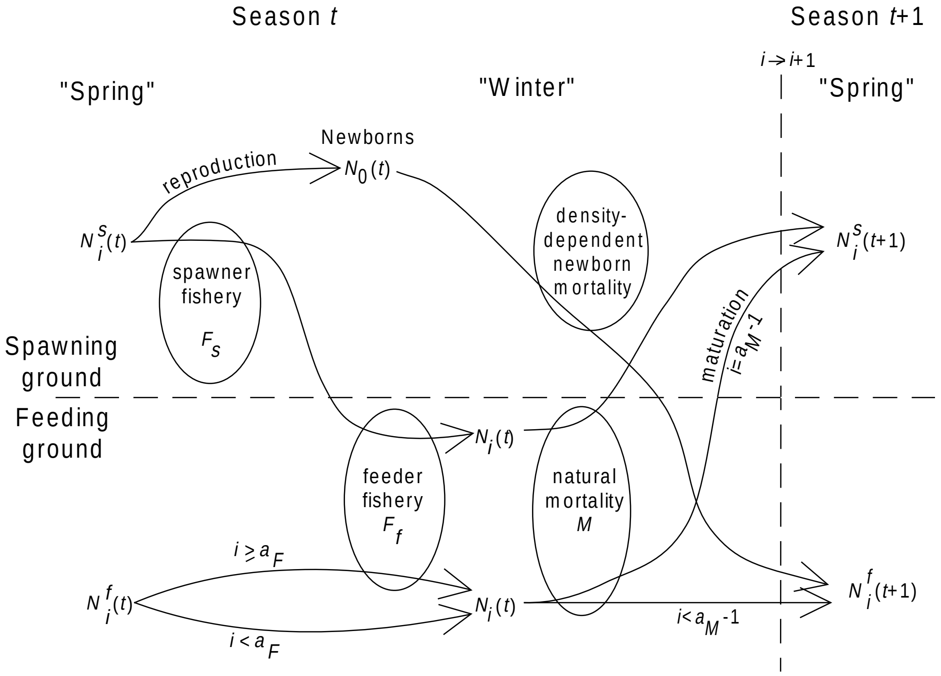

Figure 1: Schematic representation of the age- and stage-structured population dynamics model for the Northeast Arctic cod. N_i denotes the size of age-class i at the feeding grounds during late season, after fishing but before natural mortality. Superscripts s and f refer to the abundances at the spawning and feeding grounds (respectively) during early season, at the time of reproduction. Mature fish (age $\geq a_M$) are harvested at spawning grounds with rate F_S. Both mature and immature fish at least a_F years old are harvested at feeding grounds with rate F_F.

giving rise to a phenomenon called evolutionary cycling or Red Queen dynamics (Marrow et al. 1992; Dieckmann et al. 1995).

Material and methods

Model

It is typical for many exploited marine fish stocks (e.g., cod and plaice) that because of spawning migrations of mature fish, mature and immature fish are spatially separated for some part of the year (e.g., Pitcher and Hart 1982). Moreover, juvenile fish become available for harvesting only after a certain age. This may occur because small fish can escape from the fishing gear, or because of spatial segregation. Here I develop an age- and stage-structured population dynamical model featuring these basic characteristics. The model is sketched in Fig. 1. The ordering of events (harvesting, reproduction, natural mortality) is the same as in the model of Law and Grey (1989). The model is parametrized for the Northeast Arctic cod according to Law and Grey (1988).

Let $N_i(t)$ denote the number of individuals at the feeding grounds at time t in age-class i, where $i = 0, 1, \ldots a_M, \ldots, a_{MAX}$ and a_M is the age of first reproduction. Individuals reaching age $a_{MAX} = 30$ die immediately. Assume that both mature

($i \geq a_M$) and immature fish ($0 < i < a_M$) experience the same natural mortality rate M, while newborns experience density-dependent mortality following the Ricker equation. The mature fish migrate to the spawning grounds after natural mortality has occurred. The population sizes at the spawning grounds (N_i^s) and the feeding grounds (N_i^f) after natural mortality are then given by

$$\begin{array}{lll} N_i^f(t) & = N_{i-1}(t-1)sf(N_{i-1}(t-1)) & \text{for } i = 1, \\ N_i^f(t) & = N_{i-1}(t-1)\exp(-M) & \text{for } i = 2, 3, \ldots, a_M - 1, \\ N_i^s(t) & = N_{i-1}(t-1)\exp(-M) & \text{for } i = a_M, a_M + 1, \ldots, a_{MAX}, \end{array}$$

where $s = 4.75 \cdot 10^{-6}$ is the survival probability, $f(N)$ accounts for density dependence, $M = 0.2$ is the natural mortality rate. For Ricker–type density dependence, f takes the form $f(N) = \exp(-N/K)$; here N is number of newborns and $K = 4.1 \cdot 10^{14}$ is the carrying capacity.

The mature fish at the spawning grounds produce $N_0(t)$ newborns:

$$N_0(t) = \sum_{i \geq a_M} N_i^s(t) w_i(a_M) C,$$

where $w_i(a_M)$ is age-specific weight which also depends on the age-at-maturity, and $C = 250\ g^{-1}$ is the number of (female) eggs per one gram of body weight. After reproduction, the female body weight is $(1 - P)w_i(a_M)$, where $P = 0.1$ is the gonadosomatic index, i.e. the weight of gonads relative to the total body weight (Roff 1992).

The fish at the spawning grounds are harvested after reproduction with harvest rate $F_S(t)$. This harvest rate depends on the spawning stock biomass $X_S(t) = \sum_{i \geq a_M} N_i^s(t)(1 - P)w_i(a_M)$ and the chosen harvest strategy. It is assumed that fishing imposes the same mortality rate on all age-classes. Thus, the number of fish returning to the feeding grounds is $\sum_{i \geq a_M} N_i^s(t)\exp(-F_S(t))$, and the yield from the spawner fishery is $\sum_{i \geq a_M} N_i^s(t)(1 - \exp(-F_S(t))(1 - P)w_i(a_M)$.

Let $F_F(t)$ denote the harvest rate at the feeding grounds, and a_F the age at which the fish become susceptible to fishing gear. The harvest rate varies from year to year and depends on the harvest strategy and the stock biomass

$$X_F(t) = \sum_{i \geq a_F}^{a_M - 1} N_i^f(t) w_i(a_M) + \sum_{i \geq a_M} N_i^s(t) w_i(a_M)\exp(-F_S(t)),$$

where the first and second terms are biomass of immature and mature fish, respectively. The population size after the harvesting is

$$\begin{array}{lll} N_i(t) & = N_i^f(t) & \text{for } i = 1, 2, \ldots, a_F - 1 \\ N_i(t) & = N_i^f(t)\exp(-F_F(t)) & \text{for } i = a_F, a_F + 1, \ldots, a_M - 1 \\ N_i(t) & = N_i^s(t)\exp(-(F_S(t) + F_F(t))) & \text{for } i = a_M, a_M + 1, \ldots, a_{MAX}. \end{array}$$

The yield from the feeder fishery is

$$\sum_{i \geq a_F}^{a_M - 1} N_i^f(t)(1 - \exp(-F_F(t)))w_i(a_M) + \sum_{i \geq a_M} N_i^s(t)(1 - \exp(-F_F(t)))w_i(a_M),$$

where the first term represents immature fish and the second term adults. The body weights $w_i(a_M)$ were obtained from a growth model for Northeast Arctic cod by Law and Grey (1989). The earlier a fish matures, the smaller is its weight-at-age after maturation.

Simulation procedures

Extinction occured if the spawner population size went to zero. The youngest harvested age class (a_F) was set to four years. Age-at-maturity is taken as the evolving trait (i.e. σ in the section 'Evolutionarily optimal life history strategies'). The age-at-maturity prior to evolutionary change was six years. Resident populations were initiated with a population size well above the carrying capacity, and were let to stabilize for 2000 generations. The yield was the determined over 1000 generations. In evolutionary simulations, age-at-maturity was allowed to take values between four and 15 years. The different mutant types were introduced as single newborn individuals to the resident population, and were traced for 5000 generations. A resident type is an ESS, if all mutants have negative invasion exponent ρ in the environment set by the resident population. If no such type did exist, the coexisting types were determined with the aid of pairwise invasibility plots (Geritz et al. 1998).

Stochasticity was introduced into the model in two ways. First, it was assumed that newborn survival was stochastic: $s := s\epsilon_s$ with ϵ_s a normally distributed random variable with mean one and standard deviation 0.2. Second, it was assumed that stock size estimate was inaccurate, such that if $X(t)$ is the real stock size, annual quota was based on value $X(t)\epsilon_x$ with ϵ_x a normally distributed random variable with mean one and standard deviation 0.2.

Results

I first consider the performance of harvest strategies which assume a fixed fish life history. This life history is either the one observed in evolutionarily 'pristine' fish stock (evolution caused by harvesting has not yet occured), or the one observed after evolutionary change caused by a given harvest strategy has come to an end. Then I analyze the more complex scenario in which the manager changes the harvest strategy as the fish evolve.

Fixed harvest strategies

First compare the performance of constant harvest rate strategies when the fish have the original life history, first reproduction at age six. illustrates the results for three different submodels: deterministic model, stochastic model with variable newborn survival, and stochastic model with variable newborn survival and inaccurate stock size estimate. When fishing is confined to the feeding grounds (right panels), all the three submodels result in virtually identical relation between sustainable yield and harvest rate. The only major difference occurs for harvest rates high enough to result in almost zero yield: deterministic models may predict that the population is viable, while stochastic models predict extinction. Maximum sustainable yield is obtained with the relatively low harvest rate $F_S = 0.25$ in all models. This result also holds if geometric instead of arithmetic average is used.

Irrespective of harvest strategy, harvesting at the feeding grounds selects for maturation at the earliest possible age (age four). The ESOHS is the same as the optimal harvest strategy of fish stock with the original life history. As a consequence

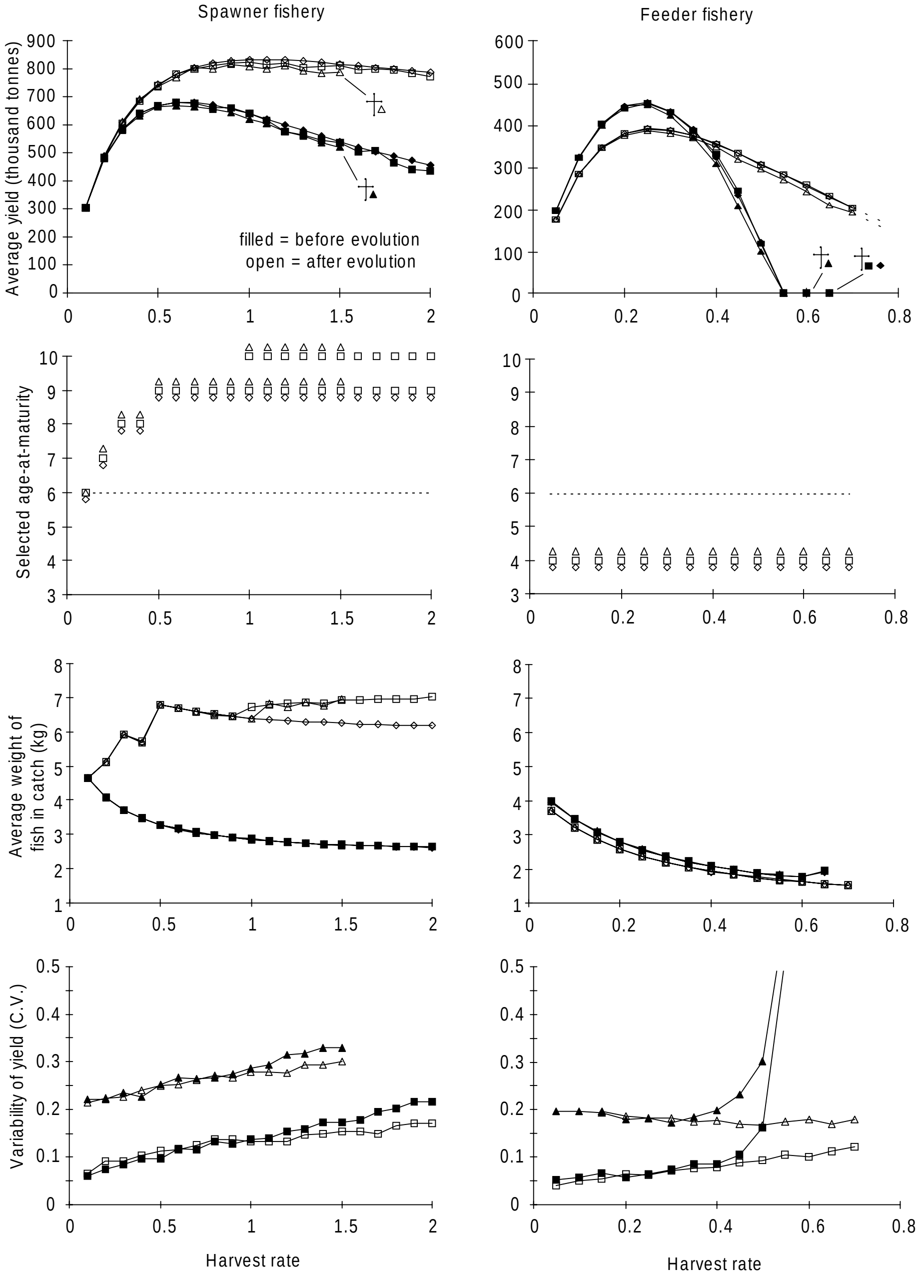

Figure 2: Sustainable yield in the spawner fishery (selective harvesting of only mature individuals after spawning) and in the feeder fishery (unselective harvesting of immature and mature fish) for different constant harvest rate strategies. Filled symbols indicate situation for original life history maturing at the age six. Open symbols are for life histories selected by given harvest rates. Different shapes of symbols indicate different models: ◇=deterministic model, □=stochastic model with noise in newborn survival and △=stochastic model with noise in newborn survival and inaccurate estimate of stock size. Crosses indicate that greedier harvest strategies result in extinction. Harvesting at the spawner fishery selects for delayed maturation and results in increased sustainable yield and average weight of caught fish, and decreased variation in annual catch. Harvesting at the feeding grounds selects for earlier maturation which causes sustainable yield to decrease and a minor decrease in fish weight.

of evolutionary change in the life history, however, the MSY decreases by about 15 %. At the same time, the average size of fish in the catch also decreases. For low harvest rates, the variability of yield remains virtually unaffected by evolutionary change. However, for high harvest rates the yield is more stable after evolutionary change.

If harvesting is confined to the spawning grounds instead of to the feeding grounds, the fish stock can sustain much higher harvest rates, and the MSY is considerably higher (Fig. 2, left panels). Even for very high harvest rates, the risk of extinction is negligible within reasonable time horizons. This result, however, rests on the assumption that harvesting occurs after reproduction. Moreover, if the stock size estimate is inaccurate, harvesting in spawning grounds can cause extinction.

Harvesting at spawning grounds selects for delayed maturation (Fig. 2). In the deterministic model, the evolutionary stable maturation age is nine years if harvest rate is 0.5 or higher. The evolutionary dynamics are more complex in stochastic models: an evolutionary branching leads to coexistence of types maturing at ages nine and ten. Later maturation results in dramatic changes in sustainable yield: the MSY, attained with an ESOHS, increases by over 20 %. At the same time, there is a considerable increase in the average weight of fish in the catch. Variability in annual catch changes very little.

The MSY obtainable from feeder or spawner fishery is approximately the same for both constant stock size and constant harvest rate strategies This result holds for both original life history, and for the life history selected by an ESOHS (maturation at age nine in deterministic model and ages nine and ten in stochastic models). However, the variability in the annual catch is higher for constant stock size strategies, the coefficient of variation being roughly twice as high as for constant harvest rate strategies when strategies close to the optimal one are compared. For high, conservative escapement goals, the variability can be exceedingly high, though. Constant stock size strategies can also lead to closed seasons (fishing not allowed at all), but the frequency of such years is low in the vicinity of optimal strategies.

Fixed quota strategies do not allow for as high sustainable yields as the two stock-size dependent strategies (Fig. 4). In the feeder fishery, average yield increases monotonically as the quota increases, but specifying a quota which is too high results in extinction. In the spawner fishery, prior to evolutionary change, the population dynamics reaches another attractor with significantly reduced yield if the quota is set too high. Therefore, in stochastic models the concept of MSY is not well defined for fixed quota strategies: it is not possible to determine MSY, or to identify optimal harvest strategies, without first defining some acceptable level of risk.

The evolutionary consequences of harvesting with a fixed quota strategy are similar to the previous cases: in the feeder fishery, harvesting selects for earlier maturation, while the spawner fishery selects for delayed maturation. After evolutionary change, the stock is able to sustain slightly higher quotas without being driven to extinction (feeder fishery) or to low abundance with inferior yields (spawner fishery).

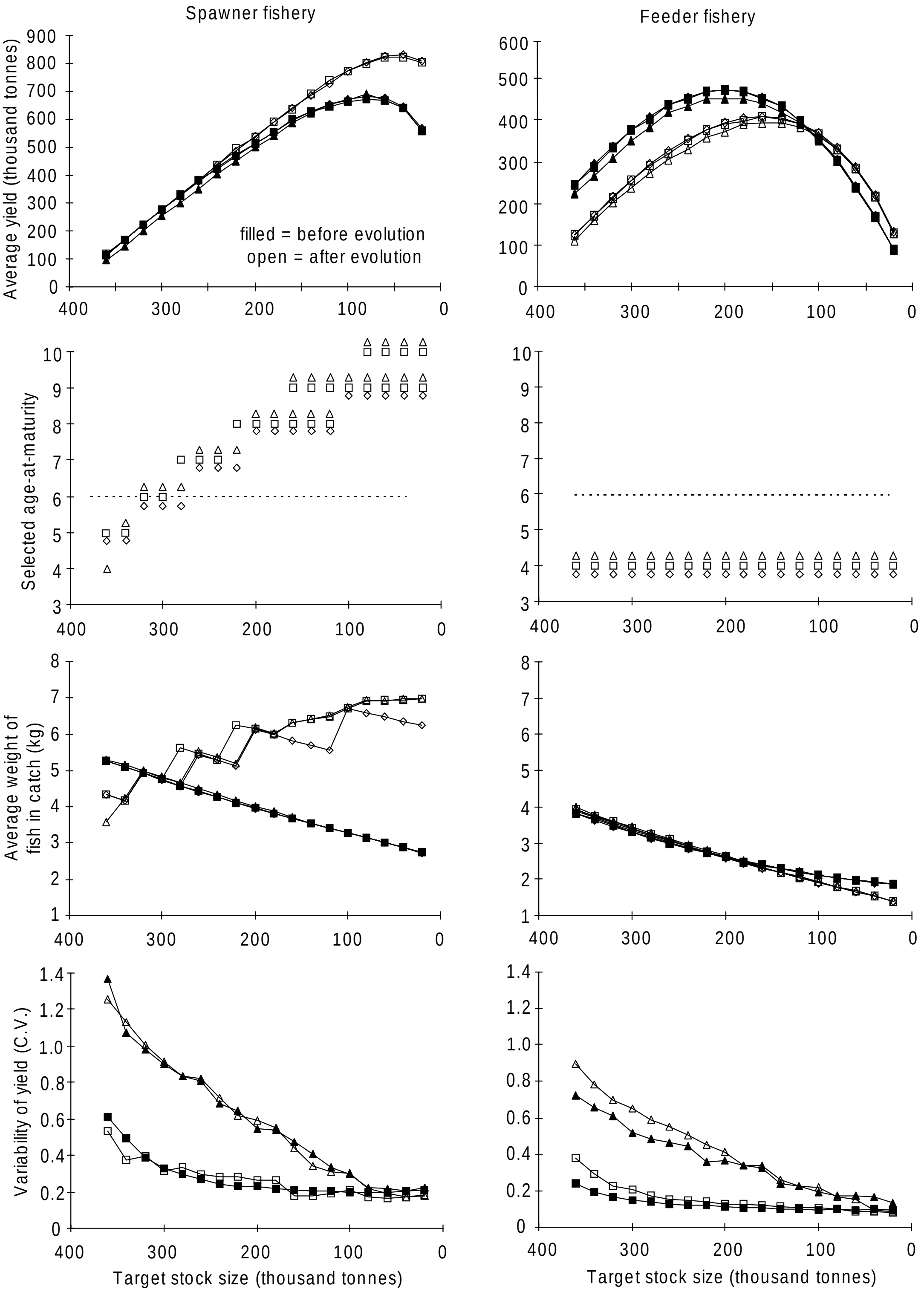

Figure 3: The performance and evolutionary consequences of harvesting with a constant stock size strategy, i.e. an excess biomass above a certain threshold is harvested. See Fig. 2 for further explanation and for comparison.

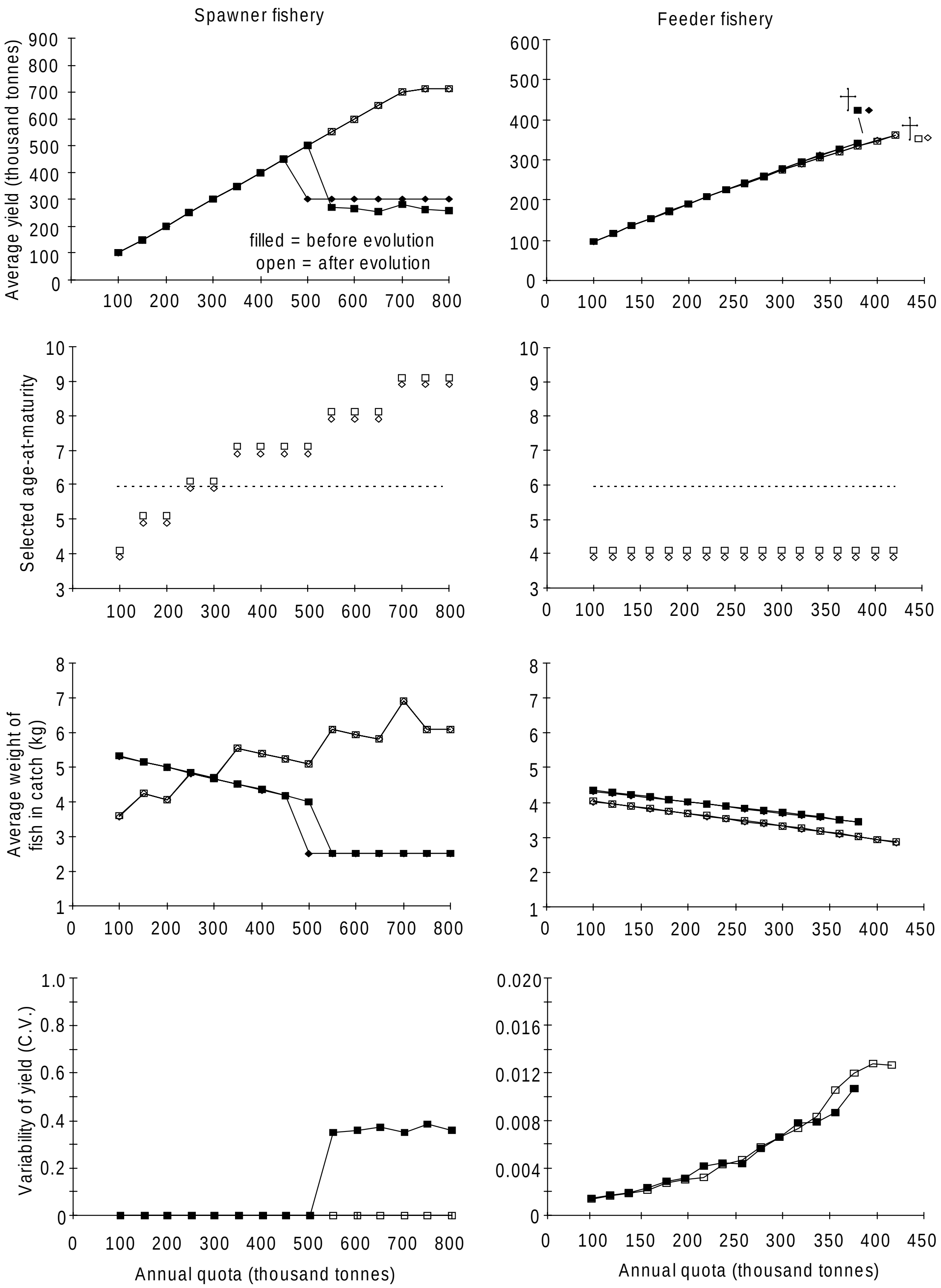

Figure 4: The performance of spawner and feeder fisheries managed with a fixed quota strategy. See Fig. 2 for further explanation and Figs. 2 and 3 for comparison.

Coevolutionary dynamics between the manager and the fish stock

Sticking to a fixed harvest strategy results in suboptimal returns either before or after evolutionary change. In reality, the manager will probably react to evolutionary change in the fish stock by adopting a new harvest strategy once a life history change affecting yield is observed. The change in harvest strategy may, in turn, induce further change in the fish life history. Thus we are facing a coevolutionary process in which the optimal strategy of one player depends on the strategy of the opponent, and vice versa.

I assume here a separation between the time scales of changes in fish life history and changes in harvest strategy: the manager chooses a new harvest strategy quickly after a successful mutant has established itself in the fish population. This is feasible if the speed of evolution is limited by availability of viable mutants. I further assume that mutation steps are small — mutants differ from the residents by only one year in their age-at-maturity.

The iterative simulation procedure for coevolutionary dynamics is as follows:

1. Initialize simulation with fish population maturing at age six ($\sigma_{res} = 6$).
2. Determine the harvest strategy η maximizing sustainable yield for the current fish life history σ_{res}.
3. Determine if the mutants $\sigma = \sigma_{res} - 1$ or $\sigma = \sigma_{res} + 1$ can invade the resident fish population, subject to harvesting with harvest strategy η, i.e. whether $\rho(\sigma, \mathbf{E}(\sigma_{res}, \eta))$ is positive or not.
4. If invasion is possible, take σ as σ_{res} and go to step (2). Otherwise, the coevolution has come to the end.

The above procedure can be easily adjusted to account for the possibility of polymorphic resident populations.

Figure 5A illustrates coevolutionary dynamics of fish population and its management when harvesting is confined to the spawning grounds and the manager adopts a constant harvest rate strategy. When the original population strategy is replaced by the one that matures one year later, the optimal harvest rate becomes higher. The age-at-maturity increases until mutants maturing at age 10 become available: they can invade a population maturing at age 9, but are not able to oust the resident. Thus, population becomes polymorphic with types maturing at ages 9 and 10 coexisting. After adjustment of the harvest strategy, coevolution has come to an end: the fish population is uninvadable by other types, and no other harvest rate would result in higher sustainable yield. Moreover, this harvest strategy is also an ESOHS, as reference to Fig. 2 confirms. Essentially similar coevolutionary dynamics are observed if the manager adopts constant stock size harvest strategy: the optimal target stock size becomes progressively smaller (implying higher average harvest rate) as the fish population evolves towards later maturation (Fig. 5B). Under both harvest policies, the average yield and the average weight of caught fish are similar and increase during the coevolutionary process (Fig. 5C-D).

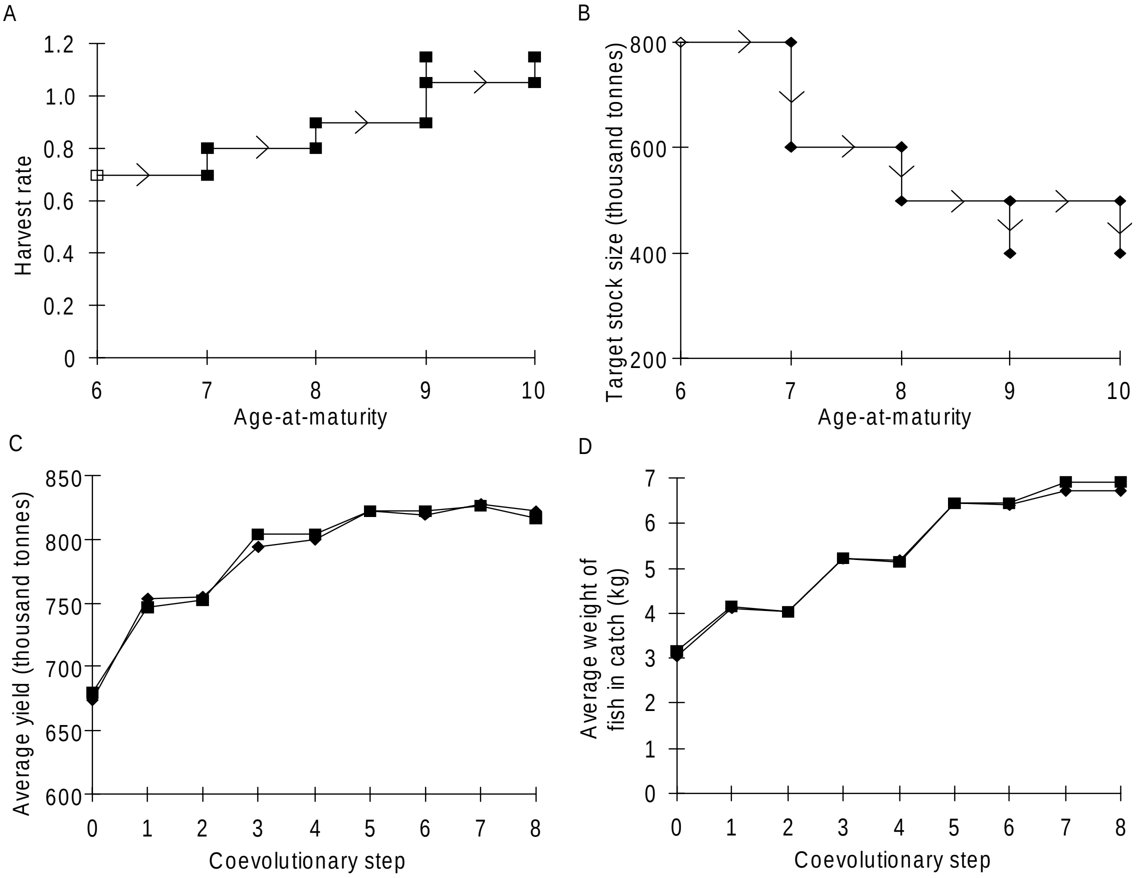

Figure 5: Coevolutionary dynamics of fish stock and the manager adopting a constant harvest rate strategy (A), or a constant stock size strategy (B) in spawner fishery (selective harvesting of mature fish). The model assumes stochasticity in newborn survival. The manager first chooses an optimal strategy (i.e. the strategy which results into MSY) for the original fish life history (open symbol). The fish stock then evolves in response to the harvesting; it is assumed that age-at-maturity can change only for one year at time. The coevolutionary dynamics reach a state in which it does pay neither for the fish nor the manager to change its strategy; at this state fish stock is polymorphic. Further, the strategy which the manager adopts is an evolutionarily stable optimal harvest strategy (see text for explanation of the term). In the course of coevolutionary change, average yield (C) and fish weight increases (D). ◇=constant harvest rate strategy, □=constant stock size strategy.

If harvesting is confined to the feeding grounds, coevolutionary dynamics follow a different path (Fig. 6). For the fish it pays to adopt earlier age-at-maturity, until minimum age-at-maturity is achieved. A manager needs not to update the harvest strategy if he adopts a constant harvest rate strategy. Under constant stock size harvest strategy, the optimal target stock size becomes smaller with decreasing age-at-maturity of fish. The coevolutionary change leads to an ESOHS in both cases (cf. Figs. 2–3). The average yield and the average weight of caught fish decrease as a result of the coevolutionary process (Fig. 6C-D).

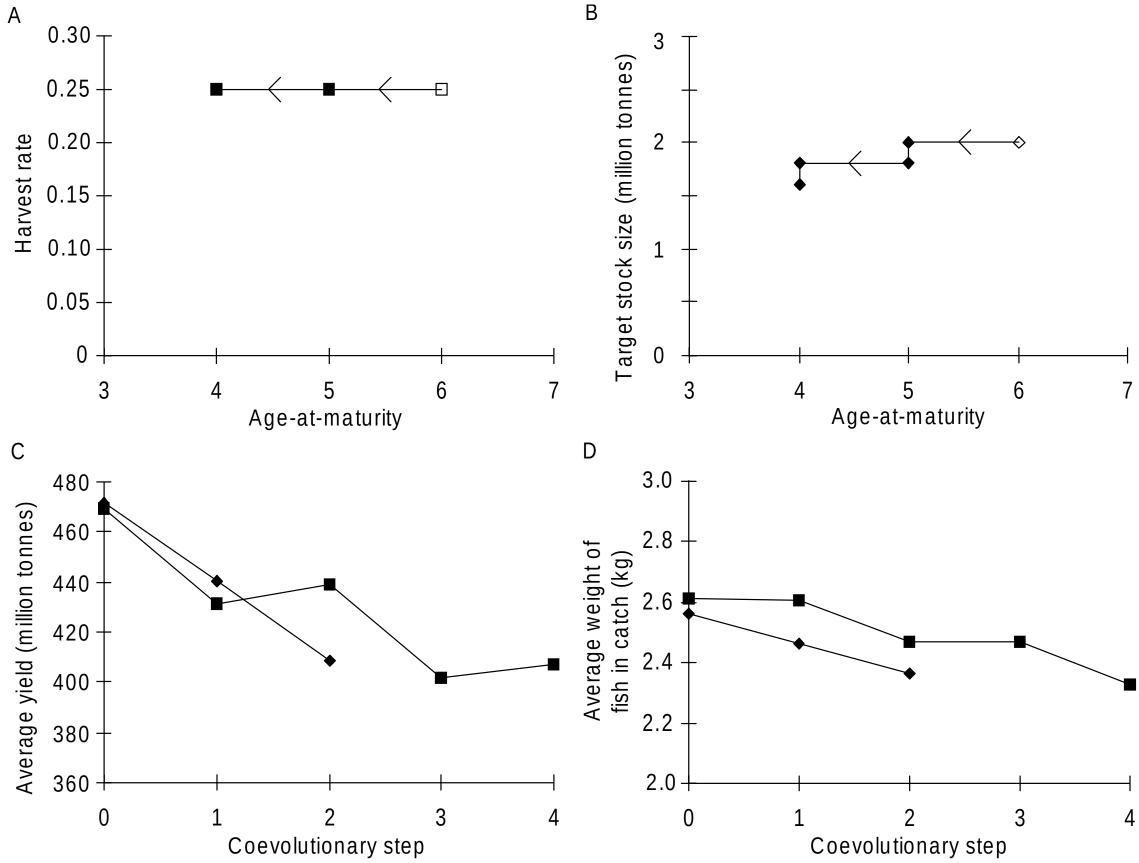

Figure 6: Coevolutionary dynamics of fish stock and the manager adopting a constant harvest rate strategy (A), or a constant stock size strategy (B) in feeder fishery (unselective harvesting of immature and mature fish). Change in average yields (C) and fish weight (D). The final harvest strategy is an ESOHS. See Fig. 5 for description of coevolutionary process.

Discussion

Selective harvesting of mature fish can cause evolutionary change that results in increased sustainable yields. Unselective fishing, however, is likely to cause evolutionary change that will make the sustainable yield decrease. These important results, already obtained by Law and Grey (1989) under the assumption of population dynamical steady state, have been shown here to extend to stochastic models. Moreover, coevolutionary dynamics of the manager and the fish stock — i.e., fish evolving in response to harvesting and the manager choosing a new optimal harvest strategy as fish stock undergoes evolutionary change — can eventually lead to an evolutionarily stable optimal harvest strategy (ESOHS) even when such strategy is not pursued in the first place. Thus, the concept of ESOHSs is not only an academic construct but it may be attained in real fisheries.

On first sight, harvesting on the spawning grounds looks clearly preferable to harvesting on the feeding grounds, where the current harvesting pressure on the Northeast Arctic cod is concentrated. Even for the current fish life history, sustainable yield from the spawner fishery is much higher than the sustainable yield from the feeder fishery. The fish from the spawner fishery are also bigger than from the feeder fishery. These differences are likely to become even more pronounced if the fish stock evolves in response to the harvesting. The only immediate drawback of fishing at the spawning grounds is that it results in slightly higher variability in annual catches than fishing at the feeding grounds. However, in reality, harvesting confined to the spawning grounds is not likely to be a real management option. The spawner fishery has two major drawbacks. First, fish are available at the spawning grounds only for a limited part of the year. Unless alternative fish stocks are available for the rest of the year, expanding fishery to the feeding grounds is a very attractive management option because it can provide year-round employment for the fishermen, and a more steady supply of fish to industry and the market. Second, fish at the spawning grounds often occur as dense spawning aggregations which are easy and economic to harvest — even if the stock abundance is relatively low (Trippel 1995). Therefore, spawner fishery is prone to overexploitation. A sustainable spawner fishery requires good knowledge of the stock combined with careful management. In the face of inevitable uncertainty, sustainability of harvesting might require such conservative annual quotas that spawner fishery might not provide higher yields than feeder fishery.

An important future direction for research is to consider size-selective harvesting, both as a tool for management and its evolutionary consequences. Another main direction is to analyze the dynamics of fishery which exploits both feeding and spawning grounds. A first step towards this direction has been made in the seminal paper by Law and Grey (1989). They found that an evolutionarily stable optimal harvest strategy in the model for the Northeast Arctic cod involves only harvesting at the spawning grounds. However, many important problems remain. One of the objectives for the management of combined feeder and spawner fishery would probably be securing steady yields throughout the year. However, high yields have to be traded off with steadiness of yields — spawner fishery yields the highest sustainable catches, which, however, are confined to a certain part of year. Taking into account the variability of catches in both fisheries makes planning of harvest strategy even harder. On the other hand, a certain fraction of annual yield needs to be caught from the spawner fishery in order to prevent evolution towards earlier maturation and decreased sustainable yield. The analysis of coevolutionary dynamics may also become more intricate. In the combined feeder and spawner fishery it is more likely that coevolutionary dynamics will not lead to an ESOHS, but will depend on initial conditions. Thus, while attaining an ESOHS in fishery confined either to the feeder or to the spawner fishery does not require evolutionarily enlightened management, the situation in the combined fishery might be more difficult.

In terms of MSY, fixed quota strategies are inferior to constant stock size and constant harvest rate strategies. However, in line with most earlier results (Hilborn and Walters 1992), constant stock size and constant harvest rate strategies perform similarly, both for the original life history, and for life histories associated with ESOHSs. Nevertheless, the same annual yield can usually be obtained with lower variability by applying constant harvest rate strategies instead of constant stock size strategies. Thus, on the basis of simulations carried out in this paper, constant harvest rate strategies are preferable over the two other classes of harvest strategies.

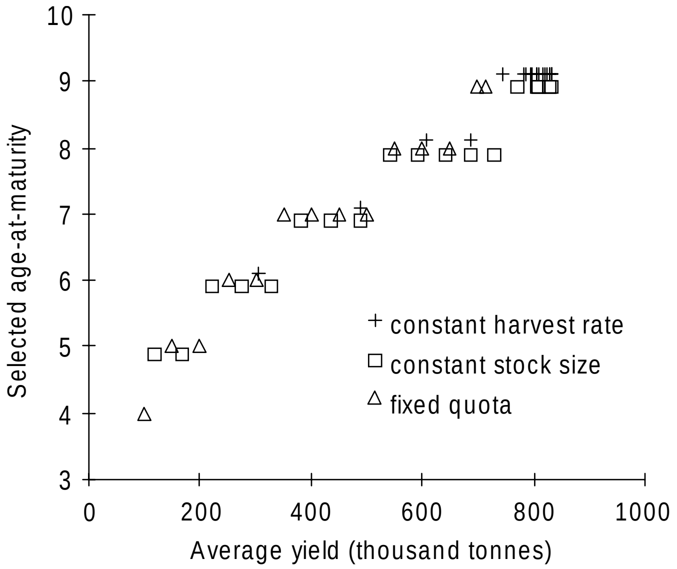

Figure 7: Comparison of the evolutionary consequences of different harvest strategies in the deterministic model.

However, the use of constant stock size strategies has been strongly advocated by Lande et al. (1995) and Engen et al. (1997). This difference in conclusions is largely due to a difference in the underlying optimality concept: in Lande et al. (1995) and Engen et al. (1997) it is yield before extinction that is being maximized. In contrast, I have assumed that the optimal strategy maximizes the yield over some limited time span during which exctinction is extremely unlikely.

Different harvesting strategies act very differently in their contribution to population regulation: Only constant stock size strategies cause fishing mortality to be positively density-dependent such that fishing becomes a regulating factor of stock size. Fishing mortality caused by constant harvest rate strategies is density-independent (by definition), and fixed quota strategies result in a negatively density-dependent mortality rate. On the basis of recent advances in life history theory emphasizing the importance of the way in which population regulation takes place (Mylius and Diekmann 1995; Metz et al. 1996a; Heino and Kaitala 1997), we might expect a priori that different harvest strategies have different evolutionary consequences. While strict comparison between the strategies is not easy, it seems, however, that the evolutionary consequences of fixed quota, constant harvest rate and constant stock size strategies are similar: strategies with similar average yield (and therefore similar average mortality rate) select for the same age-at-maturity (Fig. 7).

Trends towards earlier maturation have been observed in several fish stocks (e.g., the Northeast Arctic cod, the North Sea plaice), although it is controversial whether the observed phenotypic changes reflect genetic changes or not (Law and Grey 1989; Rijnsdorp 1992, 1993; Trippel 1995). It is known that there exists heritable variability in fish life histories, in e.g. age-at-maturity (Roff 1992; Policansky 1993). Nevertheless, decrease in length-at-age in the North Sea cod appears to have been much faster than expected on the basis of a quantitative genetics model (Law and Rowell 1993).

Whether changes in fish life histories are genetic or purely phenotypic, the results obtained here clearly show importance of taking life history information into consideration when developing sustainable management strategies. Moreover, the predictions on yields depend only on phentypic values, not genotypic. However, this issue is obviously important for predicting rate of change, and to reversibility of changes. The model presented in this paper is purely phenotypic. Thus it is inappropriate for estimating rate of change, or the time scales in which evolutionary changes begin to be significant.

Although the model presented in this paper has been formulated for the Northeast Arctic cod, the aim has been to draw attention to evolutionary consequences of harvesting in general, rather than to provide concrete management advice for a specific fishery. The qualitative results that selective harvesting of mature individuals selects for delayed maturity, and that unselective harvesting selects for earlier maturity, are fairly general and well established in life history theory (Roff 1992; Stearns 1992; Heino and Kaitala 1997).

Taking evolutionary change into account provides new options for fisheries management. It should be possible to improve sustainable yields from fish stocks by increasing the selectivity of harvesting; this appears feasible without incurring losses in sustainable yields in the immediate future. How the possibility of inducing beneficial evolutionary change — or trying to avoid unwanted change — merges with other objectives of fisheries management is a complex issue which deserves more attention in the future.

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