Fishing-induced evolution and changing reproductive ecology of fish: the evolution of steepness

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Abstract: Fishing can induce evolutionary changes in individual life history traits, leading to fish that mature smaller and younger and with larger gonads, so that they reproduce more intensely. The steepness of a stock–recruitment relationship is commonly defined as the fraction of recruitment of an unfished population obtained when the spawning stock biomass is 20% of its unfished level. We use a model of harvest-induced evolutionary change to understand how the steepness of the stock–recruitment relationship changes due to fishing. If the true spawning stock biomass is known, the stock–recruitment relationship changes little under fishing-induced evolution and there is little concern for fisheries management. When management is based on a total biomass – recruitment relationship, recruitment may be underestimated, which is also of little concern from a sustainability perspective. However, when the number of spawners – recruitment relationship is used to forecast recruitment, management practice that ignores the evolution of steepness may overestimate recruitment and therefore recommend catches that exceed safe biological limits. Using outdated maturity ogives underestimates spawning stock biomass, which results in steeper and higher stock–recruitment relationships as life histories evolve. Although of little concern for sustainability, this may pose challenges for practical fisheries management.

Résumé : La pêche peut provoquer des changements évolutifs dans les traits individuels du cycle biologique et entraîner l'existence de poissons qui atteignent la maturité à un âge plus précoce et une taille réduite, mais avec des gonades plus grandes, si bien que leur reproduction est plus intense. Le degré d'inclinaison de la relation stock–recrutement est couramment définie comme la fraction du recrutement d'une population non exploitée obtenue lorsque la biomasse du stock reproducteur est à 20 % de son niveau non exploité. Nous utilisons un modèle de changement évolutif généré par la récolte pour comprendre comment le degré d'inclinaison de la relation stock–recrutement change à cause de la pêche. Si la véritable biomasse du stock reproducteur est connue, la relation stock–recrutement change peu avec l'évolution causée par la pêche et il y a peu de préoccupations à y avoir pour la gestion de la pêche. Dans les cas où la gestion est basée sur la relation entre la biomasse totale et le recrutement, le recrutement peut être sous-estimé, ce qui est aussi peu préoccupant dans une perspective de durabilité. Cependant, lorsqu'on utilise la relation entre le nombre de reproducteurs et le recrutement pour prédire le recrutement, une méthode de gestion qui ne tient pas compte l'évolution du degré d'inclinaison peut surestimer le recrutement et ainsi recommander des captures qui dépassent les limites biologiques sûres. L'utilisation d'ogives de maturité périmées sous-estime la biomasse du stock reproducteur, ce qui produit des relations stock–recrutement plus abruptes et plus hautes à mesure que les cycles biologiques évoluent. Bien que ce soit peu préoccupant pour la durabilité, la situation peut poser des défis pour la gestion pratique de la pêche.

[Traduit par la Rédaction]

Introduction

There is increasing recognition that fishing can be a source of artificial selection and lead to evolutionary change in a variety of traits (to our knowledge, first suggested by Rutter (1902) and then revived by Law and Grey (1989), and the recent focus is exemplified by Jørgensen et al. (2007) and Dunlop et al. (2009*a*)). In particular, life history characteristics have been suggested to be especially prone to change (Ernande et al. 2004; Heino and Dieckmann 2008). Although there is still a dispute about the magnitude of such effects (Brown et al. 2008; Hilborn and Minte-Vera 2008; Andersen and Brander 2009), a precautionary approach requires that we consider the effect of fishing-induced evolu-

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tion when planning human intervention into marine ecosystems (Jørgensen et al. 2007); such an approach has been called "evolutionarily enlightened management" (Ashley et al. 2003).

Since Darwin (1859), we have understood the strong effects that artificial selection can have, and there is every reason to believe that fisheries as a source of artificial selection will act on reproductive biology (Rijnsdorp 1993). Integrating reproductive biology into scientific advice for fisheries management continues to be a challenge (Trippel 1999; Morgan 2008; Mangel et al. 2010), and in this paper, we address one important concern by analyzing how fishing-induced evolution will act on the reproductive biology of targeted species.

In this paper, we investigate how the relationship between the biomass of reproductively mature individuals (spawning stock, S) and the resulting offspring added to the population (recruitment, $R(S)$) responds to the selective pressure induced by fishing. When recruitment approaches an asymptote when stock size is large, the Beverton–Holt stock–recruitment relationship (Beverton and Holt 1957–1993)

$$(1) \qquad R(S) = \frac{\alpha S}{1 + \beta S}$$

is commonly used. In eq. 1, α is the maximum per capita productivity and β is a measure of intensity of density dependence. The functional relationship in eq. 1 can be derived by assuming that the per capita mortality rate of the recruited class is a linear function of their numbers (Beverton and Holt 1957–1993; Mangel 2006). Here, we derive the stock–recruitment relationship from more fundamental biological mechanisms using a previously published individual-based model for Atlantic cod (*Gadus morhua*) (Enberg et al. 2009). This approach allows us to study fishing-induced evolution of the stock–recruitment relationship. That is, we seek to predict the stock–recruitment relationship based on the evolutionary ecology and associated life history parameters of a species and thus understand how steepness (and the stock–recruitment relationship itself) will change in response to harvesting.

Predicting stock–recruitment relationships from evolutionary ecology is of more than academic interest. For example, strategic fisheries management requires estimates of biological reference points that often critically depend upon the nature of the stock–recruitment relationship (Brodziak 2002). The Beverton–Holt stock–recruitment relationship, in which recruitment reaches an asymptote due to increased density dependence, is widely used in stock assessments of marine fishery resources. Furthermore, the recovery of threatened or endangered populations is in large part determined by the resilience of reproduction, which in turn depends on the stock–recruitment relationship.

We use a model for Atlantic cod to illustrate our ideas because cod are commercially valuable, highly productive, and intensively exploited fishery resources and there is evidence of fishing-induced evolution in several stocks (Northeast Arctic cod (Heino et al. 2002b), North Sea cod (Yoneda and Wright 2004), and Canadian cod stocks (Olsen et al. 2005; Swain et al. 2007)). In the next section, we describe our model (first described in Enberg et al. 2009) and how it

produces the relationship between the biomass of the population or the number of spawning individuals and the number of recruits and how these change under fishing-induced evolution. Here we use the commonly accepted definition (Mace and Doonan 1988) that steepness (h) is the recruitment (R) at 20% of unfished biomass relative to recruitment at unfished biomass (S_0), that is,

$$(2) \qquad h = \frac{R(0.2\,S_0)}{R(S_0)}$$

We explore how steepness may evolve with harvesting and explain why it changes the way it does. Several stock–recruitment relationships are used in fisheries management, often dictated by the availability of data, and we therefore show changes in steepness for alternative formulations in which S may represent spawning stock biomass, total biomass, or the number of spawners. We then describe our main result: that the stock–recruitment relationship changes due to fishing-induced evolution, but that the direction and magnitude of change depends on which proxy is used for the stock indicator S. Via a sensitivity analysis, we show that our result is robust and not caused by a special parameter combination. We then discuss possible consequences of ignoring changes in the stock–recruitment relationship, with practical relevance for fisheries management.

Materials and methods

In our analysis, we use an evolving, individual-based model parameterized for a long-lived and late-maturing fish species such as Atlantic cod in its northern range. The model has already been presented in detail in Enberg et al. (2009). Here we give an overview over the main processes, but to improve readability, we have omitted equations as far as possible. The main focus is on individual bioenergetics and evolution of life history traits with consequences for population dynamics, and the model includes the processes of (*i*) growth, (*ii*) sexual maturation, according to a linear probabilistic maturation reaction norm (PMRN) (Heino et al. 2002a), and (*iii*) mating and offspring production. For growth, a model is used that includes acquisition of food and allocation to somatic and gonadic growth (Quince et al. 2008; see also Enberg et al. 2009). An allometric scaling exponent of 0.75 is used, which is suitable for piscivores. In addition, food acquisition is density-dependent (lower if the population is large, reflecting increased competition for food) and variable over time (temporally autocorrelated) and between individuals. For sexual maturation, a PMRN describes the probability that an individual of a given size and age becomes sexually mature and thus incorporates the environmental influence on maturation through phenotypic plasticity. This method is frequently used to quantify changes in maturation tendencies in wild fish populations (reviewed by, e.g., Dieckmann and Heino 2007) and in modeling studies of fishing-induced evolutionary change (Dunlop et al. 2009b). In mating and offspring production, the number of offspring that an individual produces and its probability of becoming a mate are proportional to its gonad size. Beyond this, there is no mate choice, so sexual selection is excluded. The offspring inherits the midparental trait

value with some noise added around it to give heritabilities of maturation age and size around $h^2 = 0.2$ (Gjedrem 1983).

Each individual has four life history traits inherited from its parents that therefore may evolve with time: (1) intercept and (2) slope of the linear PMRN; (3) a growth coefficient that determines growth rate in a trade-off with natural mortality and thus represents risk-sensitive foraging behavior; and (4) the target gonadosomatic index (GSI; ratio of gonads to total body mass), which determines the intensity of reproductive investment. A higher GSI implies that more of the total resources are allocated to reproduction and less to somatic growth.

The modeled individuals determine and are regulated by population-level feedback processes, including Beverton–Holt density-dependent recruitment and density-dependent growth resulting from resource competition. In addition, the feeding environment fluctuates in time to represent cold vs. warm or productive vs. unproductive periods. Finally, each individual has a risk of dying that depends on natural mortality (declining with size) and fishing mortality (sigmoid selectivity curve as is typical for trawls, with 50% selectivity at 85 cm body length).

We provide a diagram that illustrates how the processes in the model relate to one another (Fig. 1). A central assumption is that a Beverton–Holt function describes the relationship between the number of eggs spawned and the number of recruits surviving to age 1. In this paper, we report the effects on stock reproduction and steepness, as these population-level characteristics originate from evolving individual strategies, and their effects on population structure and density-dependent feedback. This analysis has both an ecological dimension, as the feedback processes depend on the number, states, and traits of individuals in the population, as well as the environmental variability, and an evolutionary dimension because selection pressures may cause the individual traits to change from generation to generation.

Thus, a key to analyzing evolutionary effects on steepness is the separation of ecological and evolutionary processes. In particular, as an evolving population is fished for increasing durations of time, individual traits gradually adapt to the fishing pressure. At different points in time, we freeze the evolutionary process and study the ecological relationships in a population with those traits. That we isolate ecological dynamics in this way does not imply that the environment needs to be constant; in our case, it is fluctuating and we focus on the average response over time. This also means that in this model, fishing is the sole driver of long-term change. Because steepness also depends on population structure, we derive the stock–recruitment relationship for two typical ecological scenarios: a fish stock currently fished (dominated by young and small individuals) or a fish stock with a moratorium implemented so that more larger and older fish are in the population.

The analysis on how fishing-induced evolution affects the steepness of the stock–recruitment relationship is carried out in the following steps (see also the flow chart in Fig. 2). First, we initialized a population with random traits and let it adapt to natural mortality alone for 200 000 years. This ensures that the population approaches an evolutionary equilibrium analogous to that of the cod stock prior to any harvesting. We then let this population adapt for a further 5000 years to natural mortality alone, and this was done 20 times so that we have 20 replicates, each starting from different initial conditions.

In step 2, the 20 replicate populations were harvested at a fixed rate of 0.4·year^{-1} using a sigmoidal size selectivity curve resembling a trawl fishery. We assumed that selectivity increases rapidly for fish with a body size of 85 cm, which corresponds to the mean body length at maturation before the start of harvesting. We stored the distribution of evolving traits after (*i*) 0, (*ii*) 50, (*iii*) 100, (*iv*) 200, and (*v*) 400 years. In this way, we built a library of 20 replicate populations of each harvest duration, 100 populations in total. By averaging over the 20 replicates, our results represent the expected mean evolutionary outcome (we observed no bimodalities in trait distributions or evolutionary outcomes).

In step 3, we then ran each population (*i–v*) without evolution for 150 years, so that offspring traits were not inherited from parents but drawn from the library from step 2. This was accomplished in the recruitment process by replacing the predicted recruits at each time step with a fixed number of seeded recruits, with each offspring's life history traits drawn randomly from the population assembled in step 2. We repeated this process 20 times for each of the population libraries above and with a fixed number of seeded recruits in nine logarithmically spaced steps up to 60 000 recruits annually (Fig. 3). The purpose of different recruitment levels was to sample the stock–recruitment curve under different population densities, and the 20 replicates were to average over ecological variability. We did so both in the absence of harvesting and with harvesting, because the stock–recruitment relationship may differ as fishing changes the population structure.

In step 4, of the 150 years simulated in step 3, we allowed 100 years to reach a fluctuating equilibrium for the population's abundance and trait distribution before we stored results and averaged them over the last 50 years of simulation. Thus, each stock–recruitment curve that we present is based on nine points of increasing population size, with each point being an average of the last 50 years in $20 \times 20 = 400$ simulations. We stored different properties of the stock (number of spawners, spawning stock biomass, and total biomass), as well as the number of recruits predicted from the modeled processes of growth, survival, and reproduction. These stored data are used to present alternative formulations of the stock–recruitment relationship.

In step 5, the steepness of each stock–recruitment curve was calculated using eq. 2 so that $h_x = R_x(0.2S_0)/R_0(S_0)$, where the subscript x on h and R indicates that we used the populations that had been adapted to harvesting for x years, and S_0 indicates that the spawning stock size is at its average level for the preharvest situation. Note that this formulation assumes that the average stock size S_0 and the corresponding average recruitment level $R_0(S_0)$ for the pristine stock are known and that steepness is defined as recruitment in the current population at a stock size of $0.2S_0$. In practice, $R_x(0.2S_0)$ was computed from the fishing-affected stock–recruitment curve using curvilinear Lagrange interpolation, and this was repeated for each duration of harvesting, i.e., $R_0(0.2S_0)$, $R_{50}(0.2S_0)$, $R_{100}(0.2S_0)$, $R_{200}(0.2S_0)$, and $R_{400}(0.2S_0)$.

In step 6, we also calculated maturity ogives (the proportion of the stock that is sexually mature as a function of age

Fig. 1. The modeling cycle is divided into individual-level and population-level processes. From the top right, in each year for all immature individuals, current age and size determine the probability of becoming mature according to a linear probabilistic maturation reaction norm (PMRN). The first two evolving individual traits (these are marked in the flowchart with numbers) are (1) the intercept and (2) slope of the PMRN. When mature, growth changes because resources also have to cover gonad maturation. Growth is also density-dependent, it fluctuates over time, and individuals experience slightly different growth conditions, and an evolving trait determines (3) the growth coefficient in a trade-off in which faster growth leads to higher mortality. Natural mortality declines with body length, whereas fishing mortality is modeled with sigmoid size selectivity as for trawling. An evolving trait also describes (4) reproductive investment implemented as the target gonadosomatic index. Offspring are produced according to gonad size, with offspring traits inherited from the parents. When these processes have been repeated for each individual, the population characteristics are updated. The total egg production determines the density-dependent juvenile survival. Recruitment feeds into population dynamics over time. The total biomass of the population determines density-dependent competition for food, which feeds back to the growth rate. By repeating this for several years, the four life history traits adapt to the fishing regime, and individual and population characteristics can be quantified and analyzed. For further model details, see the text and Enberg et al. (2009).
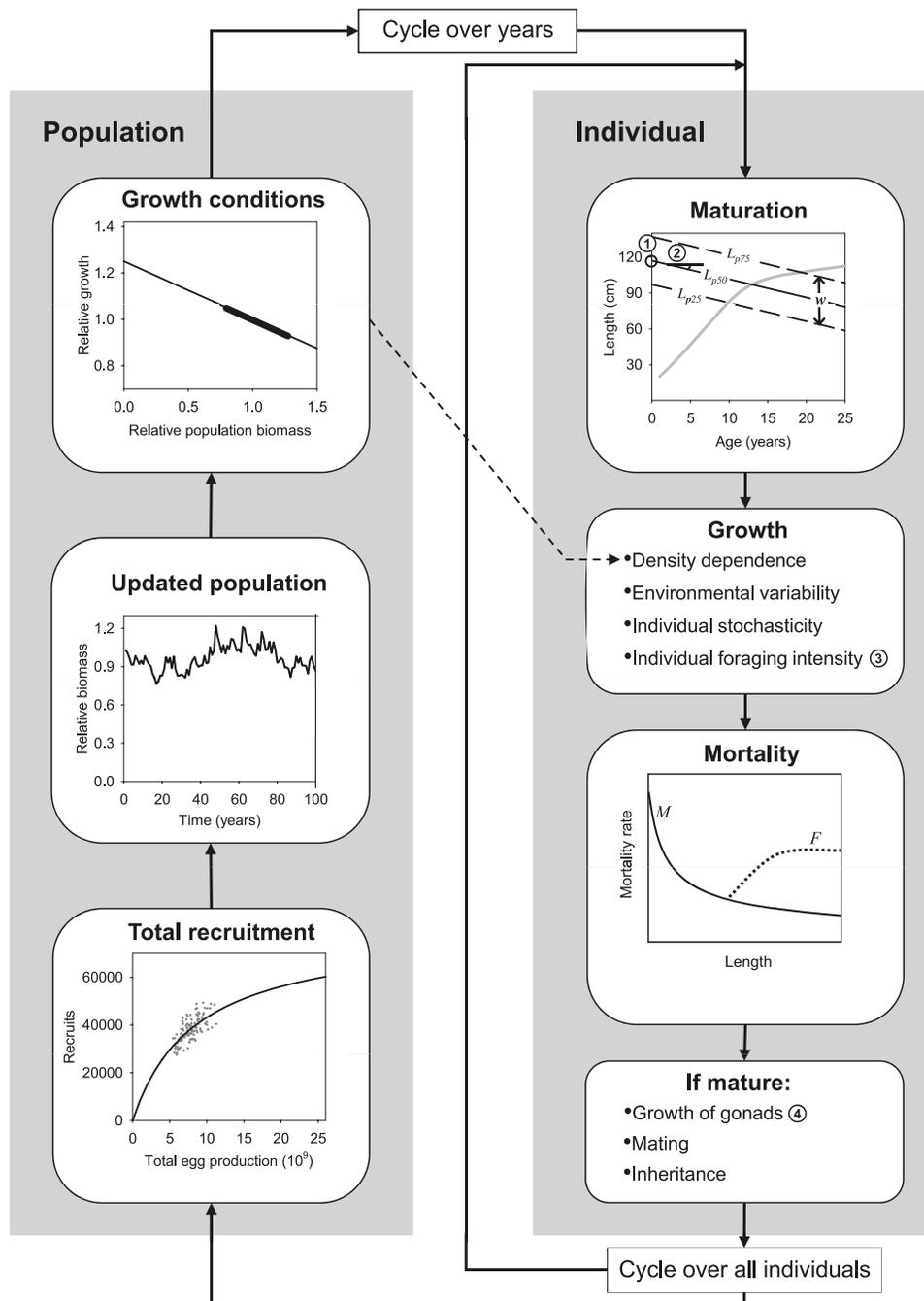
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Fig. 2. Flow scheme showing how model simulations were performed to quantify changes in the emergent stock–recruitment curves. See Supplementary data for Figs. S1–S5.[4]
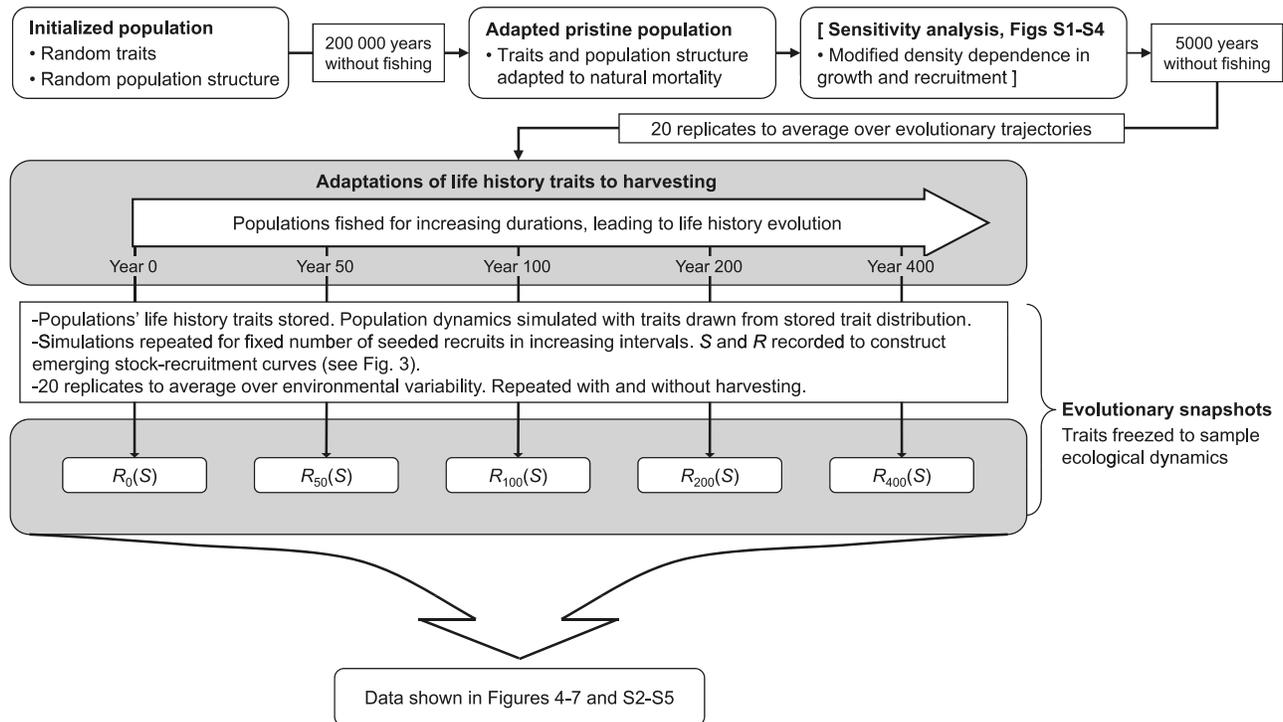
or length) for the populations to study common measures of maturation used in fisheries: age at 50% maturity (A_{50}) and length at 50% maturity (L_{50}). We found maturity ogives using a general linear model with a logit link function on proportions mature as a function of age, $o(a) = \{1 + \exp[-\beta(a - A_{50})]\}^{-1}$ by fitting parameters β and A_{50}, and correspondingly for size, $o(l)$.

Finally, in step 7, we tested a common source of error in practical fisheries management, i.e., using outdated maturity ogives to calculate SSB from survey data on population size or age distribution. To do this, we used the preharvest maturity ogives for calculating spawning stock biomass based on numbers at age (in years) or length (in bins of 2 cm) combined with average weight at age or length. Thus, if $n(a)$ denotes the number of fish at age a, $o(a)$ denotes the proportion mature at age a, and $w(a)$ denotes the mean weight of fish at age a, then

$$(3) \qquad \text{SSB} = \sum_a n(a) \cdot o(a) \cdot w(a)$$

The rationale here is that $n(a)$ and $w(a)$ are often routinely monitored in research surveys, whereas $o(a)$ often requires more thorough analyses of gonad stage and is updated less frequently. By using old data (from the pristine stock) for maturity, i.e., $o_0(a)$ but updated observations as the stock evolves, for example, $n_{100}(a)$ and $w_{100}(a)$, we can thus quantify the consequences of using old maturity data. We used an analogous formula for data stratified by length rather than by age.

The sensitivity of our results to the assumptions that we have made for the strength of density dependence in growth

and recruitment are given in Supplemental Figs. S1–S4.[4] We also evaluate consequences of using outdated maturity ogives when estimating SSB from surveyed age or length distributions (Supplemental Fig. S5)[4].
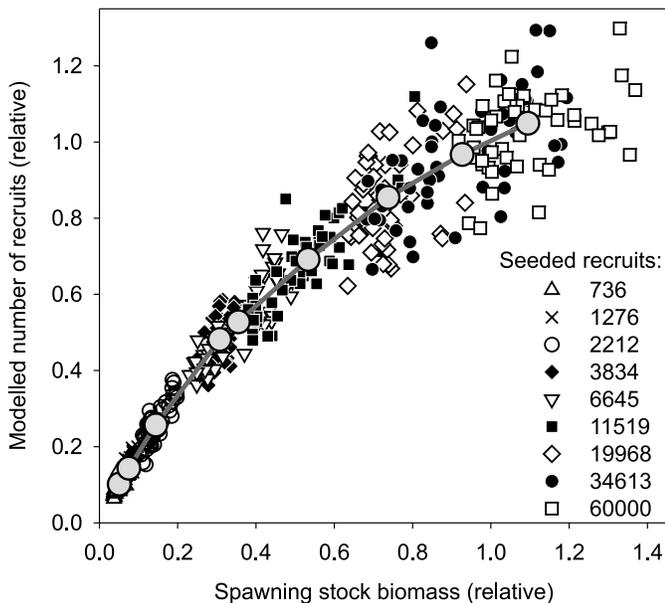
Results

Evolution of stock–recruitment relationships

Fishing-induced evolution has consequences for the stock–recruitment relationship, but the direction and magnitude of the change depends on the type of stock–recruitment relationship used (Fig. 4). The underlying cause that explains these systemic changes relates to evolution of the population's life history traits. The most dominant change in this model was that fishing induced evolution toward earlier maturation, which increased the proportion of the total biomass that is mature. If total stock biomass is used as proxy, a larger proportion of it will reproduce, and recruitment will therefore become higher with time. This explains the increasing steepness that our model predicts for the total stock biomass – recruitment relationship (Fig. 4a). Here, fishing-induced evolution lifts the entire stock–recruitment relationship over time, and the slope close to the origin becomes steeper (Figs. 4a, 4d).

In contrast, when spawning stock biomass is used as proxy, the stock–recruitment relationship remains almost unchanged (Figs. 4b, 4e). This is because the efficiency with which mature fish produced gonads and fertilized eggs varies much less. A tonne of spawning stock biomass produces roughly the same biomass of gonads and approximately the same number of fertilized eggs, even when life history

Fig. 3. Example of how each stock–recruitment curve was produced by using different fixed numbers of seeded recruits to sample different regions of the curve, corresponding to different population densities. During population simulations, the stock proxy (here spawning stock biomass) and the model's predicted number of recruits were recorded and are plotted here. Evolutionary trait inheritance was turned off when these curves were produced so that each offspring received the traits of a random individual from a stored population that represents a frozen point in time. The symbols represent different fixed numbers of seeded recruits (see inset legend), and the line is drawn between the average value (shaded circles) of each recruitment level. In Figs. 4 and 7 and in Supplemental Figs. S2–S4,[4] only the average lines are shown. The example here is recruitment of the pristine population, $R_0(S)$, without harvesting.

evolution results in SSB consisting of smaller individuals. Therefore, if one can keep track of the part of the total biomass that is sexually mature, then that proxy will remain a pretty accurate predictor of recruitment, despite large changes in life history traits. So, although the composition of the spawning stock biomass is changing toward more numerous and smaller-bodied fish in the model, their weight-specific reproduction remains largely unchanged (Fig. 4b). It should be noted that the relationship shown here assumes that the correct spawning stock biomass is known, which requires perfect knowledge about which fish are mature; we relax this assumption below.

For some stocks such as anadromous salmonids, the spawners are counted as they return to spawn. This proxy ignores that as fish mature at smaller body size with time, they also have smaller gonads. A given number of fish will therefore produce less biomass of gonads as they adapt to fishing and, consequently, fewer fertilized eggs. This is why the number of spawners – recruitment relationship is shifted downwards with time, and the slope close to the origin becomes less steep (Figs. 4c, 4f).

Moratorium versus continued fishing

Continued harvesting on a stock has two implications. First, the repeated fishing events will take away the older

and larger individuals so that the stock is biased towards young and small fish. Second, fishing releases density dependence by removing biomass so that individuals grow faster, and when fewer spawners produce fewer eggs, the Beverton–Holt juvenile density dependence prescribes that each egg has higher survival probability. Together, released density dependence during fishing may increase the population's ability to grow. When we contrast results as they would have been observed if fishing were continued or a moratorium put in place, it is the combined role of demography and density dependence that is quantified.

The spawning stock biomass – recruitment relationship is only negligibly affected by fishing-induced life history evolution over time, but the whole relationship is less steep if observed during a moratorium (compare Figs. 4b and 4e). This is because biomass builds up during the moratorium, leading to reduced individual growth and reduced survival from egg to recruit. As a consequence, the same recruitment level requires a higher spawning stock biomass in the moratorium scenario compared with when fishing is continued.

The total biomass – recruitment relationship is less influenced by life history evolution during the moratorium scenario than during the fished scenarios (Figs. 4a, 4d). Prior to life history evolution, the size-selective fishing takes out mostly mature fish, and fishing therefore has a large effect on reproduction (the solid lines are very different between Figs. 4a and 4d). When the population has adapted to fishing, the fish mature smaller and spend more of their life below harvested sizes. In that case, continued fishing has less impact on the mature proportion, and the total stock biomass – recruitment relationship is more similar between the moratorium scenario and fished scenarios (compare dotted lines in Figs. 4a and 4d).

With number of spawners as proxy, evolution leads to stock–recruitment curves that are less steep close to the origin for both the moratorium and the fished scenarios (Figs. 4c, 4f). Populations adapted to harvesting mature at smaller size and therefore stay below the harvested sizes for more of their life. A given number of spawners will therefore be of smaller size, have smaller gonads, and produce fewer recruits as evolution proceeds; this is why the number of spawners – recruitment curves become less steep.

Changes in steepness parameter h

The changes in the stock–recruitment relationships can be quantified by the steepness parameter h (eq. 2; Fig. 5). Steepness changes the least when actual spawning biomass is known, becomes steeper when the stock is expressed in terms of total biomass, and becomes less steep if the number of spawners is used. Regardless of whether fishing is continued or stopped, the change in steepness is roughly the same if spawning stock biomass or number of spawners are used as proxies in the stock–recruitment relationship. When total stock biomass is used, however, the increase in steepness is more pronounced if fishing continues (compare Figs. 5a and 5b).

The longer the population is subject to harvest, the more life history evolution will take place, and thus the greater the change in steepness will be. Moreover, the changes in steepness are most rapid early on, and for all three stock–recruitment relationships, the value of steepness changes

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Fig. 4. The consequences of fishing-induced evolution for stock–recruitment relationships depend on the stock property that is surveyed and used to monitor and predict recruitment (indicated on the *x* axes). These panels show recruitment as a function of (*a* and *d*) total stock biomass (age 2+), (*b* and *e*) spawning stock biomass, and (*c* and *f*) number of spawners. In the upper panels, the stock is being fished while the sampling is carried out, whereas in the lower panels, there is no fishing during sampling, corresponding to observations that might be made during a fishing moratorium. All values are normalized relative to the mean equilibrium value of the proxy and recruitment prior to life history evolution and in the moratorium situation (pristine stock dynamics).
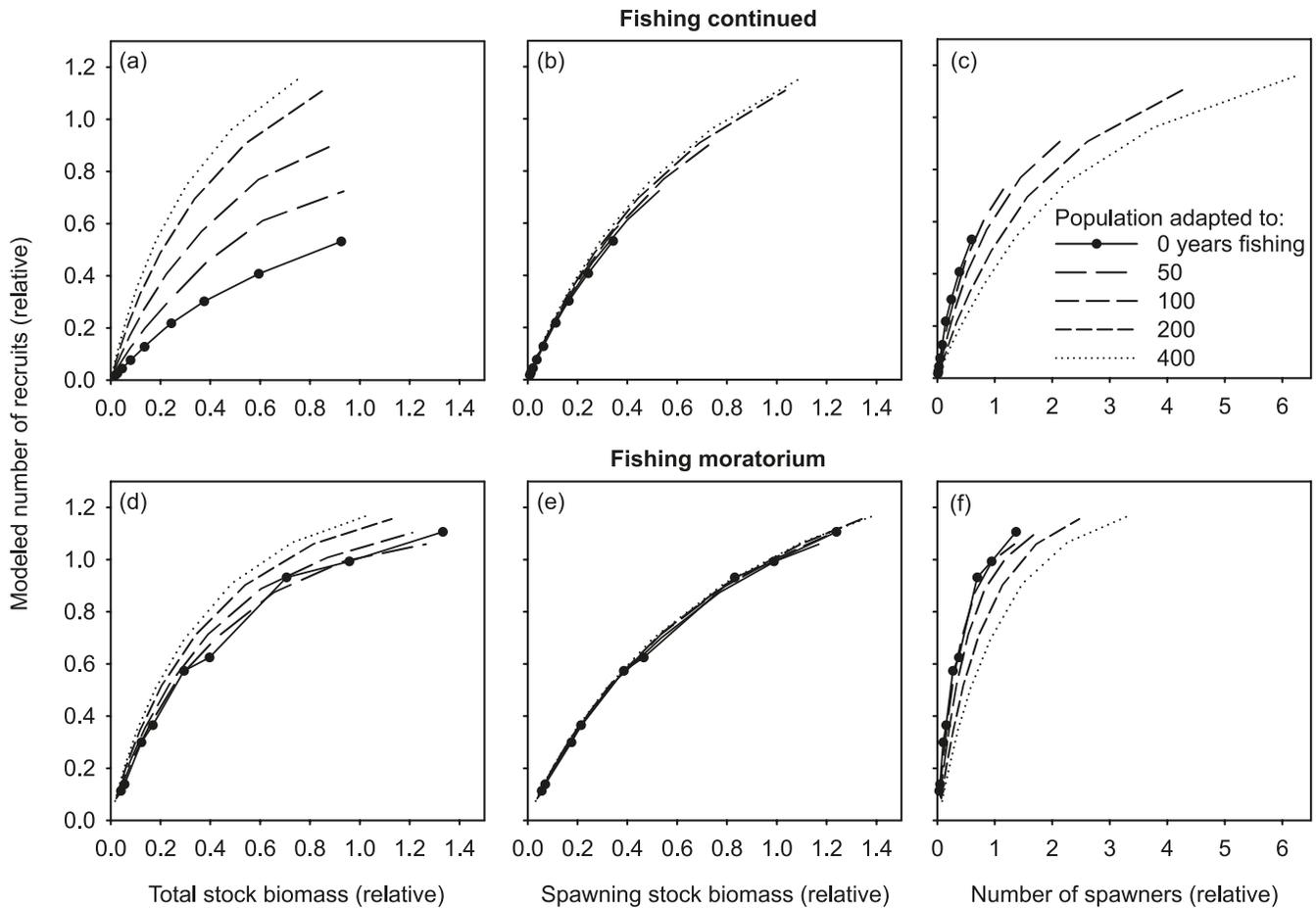

Fig. 5. Fishing-induced evolution of the steepness parameter *h*, quantified for different stock–recruitment relationships, as observed (*a*) if fishing continues on the stock or (*b*) if a fishing moratorium is implemented. The model population was harvested for increasing duration (*x* axis), and population dynamics were analyzed to quantify the stock–recruitment curve and the steepness parameter. The different lines correspond to stock–recruitment relationships that use different proxies for parental stock (triangles and dotted lines, total stock biomass; circles and solid lines, spawning stock biomass; squares and broken lines, number of spawners).
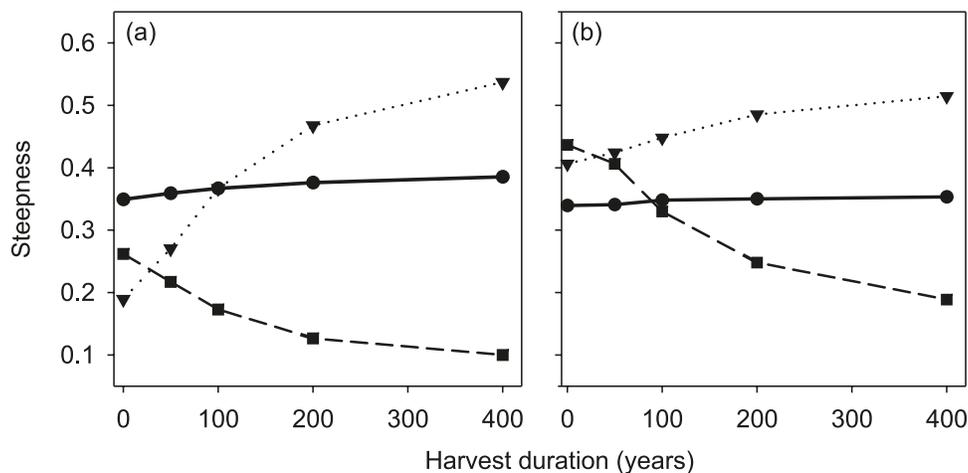
Fig. 6. (*a*) The development of mature (spawning stock) biomass and immature biomass due to demographic changes and evolution of life history traits; (*b*) the same presented as proportion of total biomass. In (*a*) and (*b*), there is no fishing prior to year 0, and the preharvest equilibrium is shown for 400 years to illustrate the level of interannual variability in the model. The biomass changes are caused by maturation evolution, as evidenced by declining (*c*) age at 50% maturity (A_{50}) and (*d*) length at 50% maturity (L_{50}) as a function of the duration of harvesting. Shaded dots show values that would be seen if fishing were continued, whereas solid dots show the values that would be observed during a moratorium.
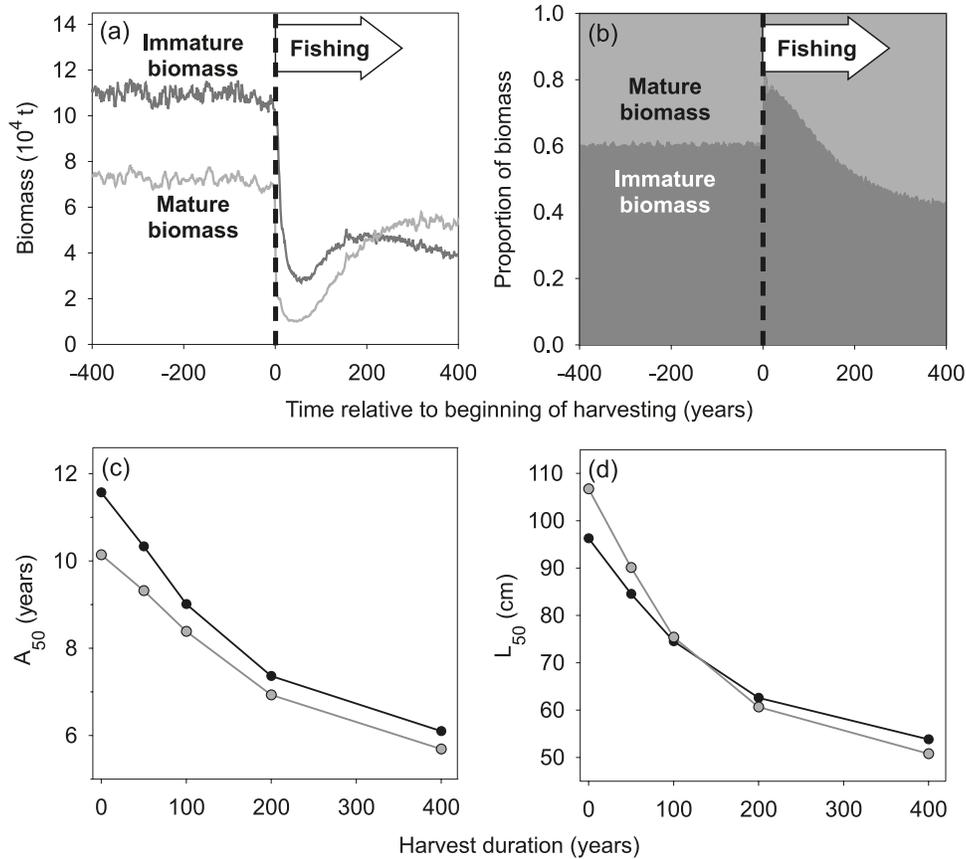
more slowly with time. However, new equilibria are not reached even after 400 years of harvesting.

Life history evolution and changing steepness

The evolutionary changes in steepness and the stock–recruitment relationships can be understood by investigating population dynamics and individual life history traits. When harvesting begins on a stock, population size declines, especially the number of old and sexually mature fish (Fig. 6*a*). After some period of harvesting, however, total stock biomass and mature biomass begin to increase (Fig. 6*a*). This happens because the life history traits evolve adaptations to the new fishing regime. In particular, earlier maturation allows individuals to mature before they are fished, and fish that mature smaller also spend more time below the minimum size limit in the fishery. The proportion of the stock that is comprised of mature fish increases over time, from 40% in the preharvest equilibrium to around 60% after a few centuries of harvesting (Fig. 6*b*). The underlying evolutionary changes in life history traits in the model cause age and length at maturation to decline (Figs. 6*c*, 6*d*), and the fish also have larger gonads for a given size and grow faster. Compared with the situation before harvesting, these evolutionary changes in individual life history traits lead to fish that mature smaller

and younger and with larger gonads, so that they reproduce more intensely.

When maturation is surveyed infrequently

Thus far, we have used the model output directly, which means that we assume perfect knowledge about the stock. One particular source of error is when old maturity ogives are used to estimate spawning stock biomass. To mimic this situation, we used a maturity ogive from the pristine stock (before harvesting) to calculate spawning stock biomass from age or length distributions (using eq. 3), although evolution of the stock's life history traits would cause changes in the maturity ogives. The spawning stock – recruitment curves estimated in this way become steeper over time, regardless of whether age or length ogives are used and regardless of whether fishing is continued or a moratorium implemented (Figs. 7*a*–7*d*). This result shows stark contrast to the situation in which accurate information about stock maturity is known; there the spawning stock – recruitment relationship is essentially constant over time (Figs. 4*b*, 4*e*).

A note of caution should be added: the length-based maturity ogives are statistically fitted logistic curves assuming a sigmoid shape, but this functional form does not fit very well with the actual proportions mature as a function of length (for examples, see Supplemental Figs. S5*b* and

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Fig. 7. When the spawning stock biomass is calculated using a maturity ogive derived from the pristine stock, the SSB–recruitment curve becomes steeper as evolution progresses with the duration of harvesting. The SSB has been calculated based on an age-based maturity ogive in (*a*) and (*b*) and on a length-based maturity ogive in (*c*) and (*d*). (*e*) and (*f*) The consequences for steepness are shown, with circles and solid lines representing steepness when an outdated age-based maturity ogive is used, and triangles and dotted lines representing length-based ogives. In (*a*), (*c*), and (*e*), observations are made on a stock that is continuously fished; in (*b*), (*d*), and (*f*), there is a fishing moratorium. The temporal changes in the maturity ogives themselves are shown in Supplemental Fig. S5.[4]
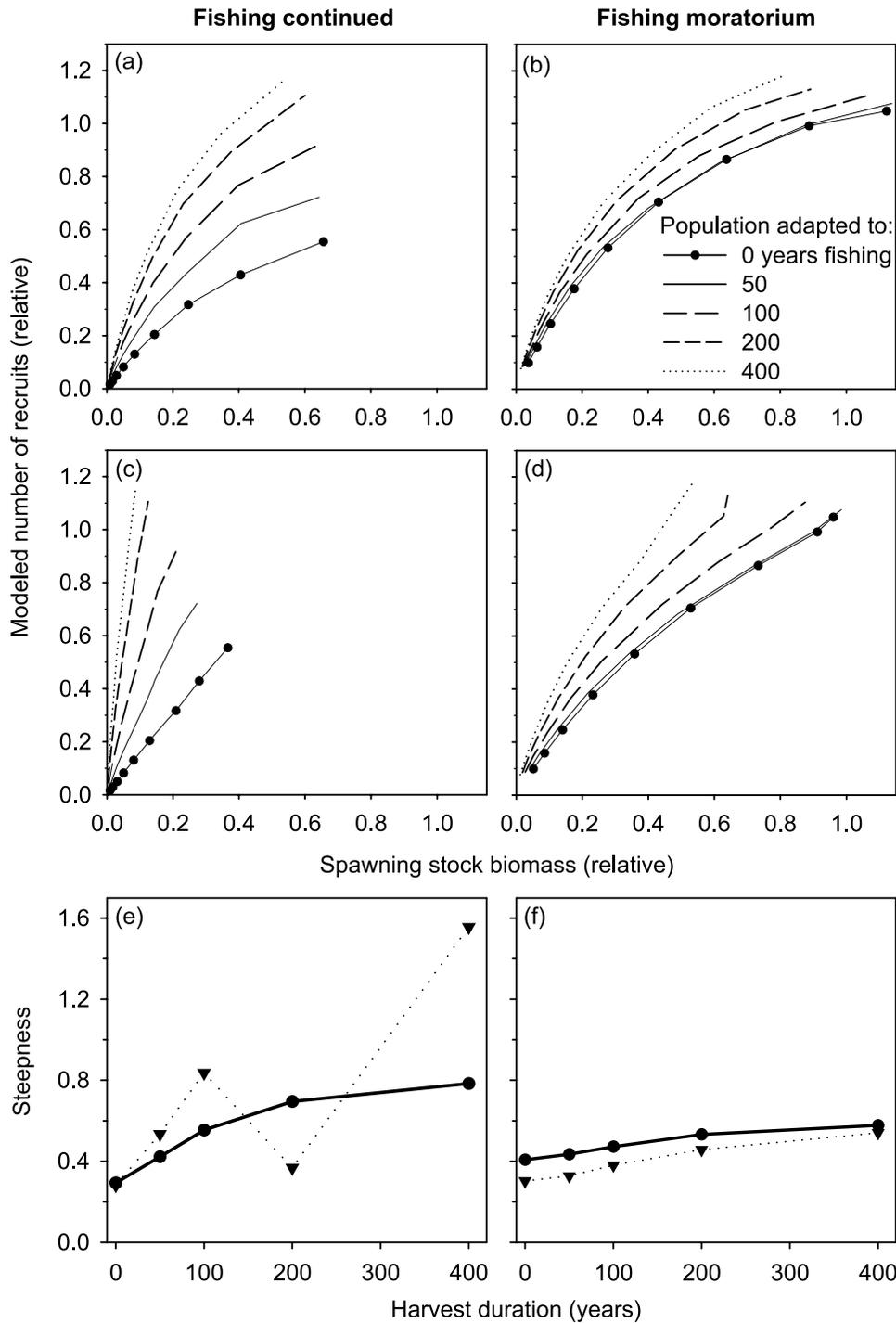
S5*d*[4]). The poor fit results in spawning stock – recruitment curves that are unrealistically high when length-based ogives are used and makes estimation of steepness difficult and potentially inaccurate (Figs. 7*e*, 7*f*). The same complications do not apply to the age-based maturity ogives in our model.

Discussion

Human interventions may change the environment to which organisms adapt in ways that trigger evolutionary processes on multiple time scales (Reznick and Ghalambor

2001). These adaptations may be quick and take place within decades (Hendry and Kinnison 1999; Reznick and Ghalambor 2001). For fish, one element of their environment that has changed dramatically in recent times is that the harvest rates imposed by commercial fishing may be up to four times higher than natural mortality rates (Mertz and Myers 1998). This led Rijnsdorp (1993, p. 391) to call fisheries "a large-scale experiment on life-history evolution". A recent meta-analysis identified harvesting as producing rates of phenotypic change roughly three times higher than other anthropogenic interventions (Darimont et al. 2009), and another meta-analysis found that life history changes were of larger magnitude in fish populations subject to more intense harvesting (Sharpe and Hendry 2009). As time series data and tools to analyze them have become available, life history traits and, particularly, age and size at maturation have been identified as particularly prone to change (Heino and Dieckmann 2008). These traits are central to fish population dynamics as they determine when fish become reproductively active and, therefore, how efficient the population is at producing new recruits. Such fishing-induced life history evolution may therefore be crucial for medium- and long-term development of yield and for fisheries management (Jørgensen et al. 2007).

Stock–recruitment relationships

In most cases of practical fisheries management, it is impossible to quantify individual reproduction directly. Instead, over many years, one records the relationship between population-level characteristics and recruitment to the stock, and management then aims to keep the population-level measure within limits that ensure acceptable recruitment (Fowler 2009). Examples of such population-level characteristics used in fisheries management include total stock biomass, spawning stock biomass, and number of spawning fish. Thus, although the aim of fisheries management is to ensure sustainable levels of recruitment, this is often obtained by focusing management on a proxy that is easier to quantify during surveys. An additional advantage is that there is often a time lag between the population-level measure and recruitment, so this approach allows for forecasts for the near future.

The stock–recruitment approach rests on the assumption that the past relationship between the population-level proxy and recruitment remains unchanged, so that the stock's past behavior describes what it will do now and in the near future. Because fishing-induced evolution has potentially potent effects on individual life history traits, that assumption may be violated.

Consequences of changing steepness

In this paper, we used an individual-based model for fish life history evolution to study the evolution of reproductive characteristics as they respond to harvesting. In particular, we quantified changes in the stock–recruitment relationship and the steepness parameter that is often used in fisheries management.

If the stock–recruitment relationship becomes steeper with time, then recruitment will be higher than predicted from the population-level proxy. From a sustainability perspective, this is of little concern because recruitment will be better than believed by the managers. In practical fisheries management, this may still cause conflicts, because fishermen

will observe the stock as repeatedly being larger and recruitment higher than that forecasted by the managers. Stakeholders in the industry may then call for higher quotas, which managers may feel uneasy about because they believe that recruitment should be worse than it is. Our model suggests that this will be the case if recruitment is modeled with a total biomass – recruitment relationship or if older length- or age-based maturity ogives are used to estimate the spawning stock biomass.

The situation is more serious if the stock–recruitment relationship becomes less steep over time. Fisheries management that focuses on a proxy will then repeatedly believe that recruitment should be higher than it turns out to be. This would in turn lead managers to allow more fishing than the stock can sustain and over time could drive the stock to low levels with imminent risk of collapse. In our model, this is most likely to happen if a number of spawners – recruitment relationship is used, as is commonly done for anadromous fish that are counted as they return from sea to spawn in rivers or freshwater.

Other causes for changing steepness

It should be noted that several mechanisms not included in this model might influence the steepness of a stock–recruitment relationship. For example, in migrating species, there is often an advantage of being large because of the way that swimming costs scale with size (Roff 1988). If life history evolution causes maturation at smaller size, these fish may spend more of their energy budget on the migration and have less for the production of gonads, or they might migrate shorter distances to areas that are less favorable (modeled in Jørgensen et al. 2008). Both of these mechanisms could lower the steepness of a spawning stock biomass – recruitment relationship.

When maturity ogives are outdated

Survey data are always incomplete. In particular, it is often difficult or costly to sample individual maturity status, and spawning stock biomass may be calculated based on a maturity ogive that has been obtained earlier. The ogives used in practical fisheries management are sometimes several years or decades old. For example, the International Council for the Exploration of the Sea (ICES) used a maturity ogive from the early 1980s in their 2009 stock assessment for North Sea plaice (ICES 1983, 2009).

When fishing-induced life history evolution causes earlier maturation, the consequence of using outdated maturity ogives is that the mature part of the stock is underestimated. When the underestimated spawning stock biomass obtained in this way is plotted against recruitment, the stock–recruitment relationship will seem steeper over time. In other words, true recruitment will consistently lie above the expected level predicted from the stock assessment. This likely will lead to a conservative fishing regime in which quotas are set below what fisheries managers would have chosen if they had had a correct view of the spawning stock biomass, and from a sustainability perspective, this is of little concern.

Complications might arise when one begins to look for explanations for the unexpectedly high recruitment. Because evolutionary change is a gradual change over time, any consistent temporal trend may lead to spurious correlations and falsely be identified as the cause for the high recruitment.

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Sensitivity analyses

We tested the robustness of the model's predictions by varying two central processes: the strength of density-dependent regulation of individual growth rate and the shape of the total egg production – recruitment relationship (the sensitivity analysis is reported in Supplemental Figs. S1–S4[4]). The qualitative prediction that the change in steepness depends on the stock proxy that is used was not challenged by variation in these processes. For all parameter combinations that we tested, steepness was relatively unchanged when spawning stock biomass was used as proxy, steepness increased with total biomass as proxy, and steepness declined when the proxy was number of spawners.

All species are different, and we cannot claim that these results are general. However, it seems plausible that the model's qualitative predictions form a first expectation for species in which fishing-induced life history evolution leads to earlier maturation. A tendency to mature at younger ages and smaller sizes has been documented in a wide range of species worldwide (listed by Dieckmann et al. 2009), but there are exceptions that can be explained by the intensity and selectivity of the fishery (e.g., Engelhard and Heino 2004).

Implications for management

Fishing-induced evolution is likely to affect life history traits with implications for population-level characteristics and recruitment. Such changes may alter the stock–recruitment relationship, which is often central to stock assessment and management advice.

If the true spawning stock biomass is known, the stock–recruitment relationship changes little due to fishing-induced evolution and there is little concern for fisheries management. Monitoring of maturity status is often costly and time-consuming, however, and we fear that old or outdated maturity data are frequently used in routine stock assessments, especially for small stocks, for stock of little commercial value, or when species biology makes such monitoring particularly challenging. If maturation is changing in these stocks, increased monitoring of maturity status could improve the accuracy of stock assessments by explaining temporal trends in the stock–recruitment relationship.

When management is based on a total stock biomass – recruitment relationship, recruitment may be underestimated, which is of little concern from a sustainability perspective. The most worrisome case is the one in which the number of spawners – recruitment relationship is used to forecast recruitment and to set harvest quotas. For such stocks, current management practice may overestimate recruitment and therefore recommend catches that exceed safe biological limits.

Acknowledgments

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