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

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

Interim Report IR-09-059

Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species

Erin S. Dunlop (erin.dunlop@ontario.ca)
Marissa L. Baskett (mlbaskett@ucdavis.edu)
Mikko Heino (mikko.heino@imr.no)
Ulf Dieckmann (dieckmann@iiasa.ac.at)

Approved by

Detlof Von Winterfeldt
Director

September 2011

Propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species

Abstract

Evolutionary effects of fishing can have unwanted consequences diminishing a fishery's value and sustainability. Reserves, or no-take areas, have been proposed as a management tool for reducing fisheries-induced selection, but their effectiveness for migratory species has remained unexplored. Here we develop an eco-genetic model to predict the effects of marine reserves on fisheries-induced evolution under migration. Our model is parameterized for Atlantic cod (*Gadus morhua*) in the northern part of its range, describing a stock that undergoes an annual migration between feeding and spawning grounds. Our analysis leads to the following conclusions: (i) A reserve in a stock's feeding grounds, protecting immature and mature fish alike, reduces fisheries-induced evolution, even though protected and unprotected population components mix on the spawning grounds. (ii) In contrast, a reserve in a stock's spawning grounds, protecting only mature fish, has little mitigating effects on fisheries-induced evolution and can sometimes even exacerbate its magnitude. (iii) Evolutionary changes that are already underway may be difficult to reverse with a reserve. (iv) After a reserve is created or enlarged, most reserve scenarios result in yield losses. (v) Timescale is very important: in the wake of a reserve's creation, short-term yield losses can lead to long-term gains.

Keywords: fisheries-induced adaptive change; contemporary evolution; marine reserve; marine protected area; density-dependent growth; phenotypic plasticity; migration; Atlantic cod.

Introduction

Recent theoretical studies (e.g., Ernande et al. 2004; Thériault et al. 2008; Dunlop et al. 2009; Arlinghaus et al. 2009; Enberg et al. 2009; Jørgensen et al. 2009) and empirical assessments (e.g., Ricker 1981; Grift et al. 2003; Olsen et al. 2004; Mollet et al. 2007) have provided compelling evidence that fishing can induce evolutionary changes in key life-history traits. For example, the most commonly observed fisheries-induced trend attributed to evolution is toward earlier ages and smaller sizes at maturation (see recent reviews by Jørgensen et al. 2007; Kuparinen and Merilä 2007; Hutchings and Fraser 2008; Dunlop et al. 2009). If occurring, these evolutionary changes could cause reduced body sizes in the catch; diminish a stock's productivity, stability, and recovery potential; lead to economic loses; and take a long time to reverse (Kirkpatrick 1993; Heino 1998; Law 2000; Dunlop et al. 2009; Conover et al. 2009; Enberg et al. 2009). Therefore, managers need viable options for mitigating the unwanted evolutionary consequences of fishing. Even though the evidence for fisheries-induced evolution has triggered some lively debate in the literature (Hilborn 2006; Conover and Munch 2007; Browman et al. 2008; Heino et al. 2008; Jørgensen et al. 2008b; Kuparinen and Merilä 2008; Swain et al. 2008), the precautionary approach to fisheries management warrants that the potential consequences of evolution be carefully considered to ensure sustainable fisheries.

Marine reserves are seen as an important tool in bringing an ecosystem perspective to fisheries management, because they help preserve ecosystem structure and function, with possibly positive effects also occurring outside the reserves (Costanza et al. 1998; Pauly et al. 2002; Lubchenco et al. 2003). Moreover, by protecting a certain segment of a population from harvest, marine reserves might also reduce, stop, or reverse the evolutionary consequences of fishing. This reasoning has led some to propose marine reserves as a potential tool for managing evolving fish stocks (Conover and Munch 2002; Law 2007). Marine reserves may be expected to reduce the overall selective pressures causing, for example, earlier maturation, because they could be expected to protect a proportion of the population's individuals with genotypes coding for delayed maturation (Trexler and Travis 2000). A study by Baskett et al. (2005) supports this hypothesis. Based on the analysis of a quantitative genetic model, Baskett et al. (2005) predict marine reserves to reduce fisheries-induced selection for smaller sizes at maturation, provided the reserves are large enough relative to the target species' dispersal range. Similarly, a simple age-structured individual-based model by Miethe et al. (2009) also predicts the creation of reserves to reduce evolution of smaller sizes at maturation. Marine reserves might furthermore offer additional evolutionary benefits, such as the protection of genetic diversity (Perez-Ruzafa et al. 2006).

Compared to traditional management approaches (including size limits and effort limits), marine reserves may not enhance fisheries or provide effective protection from overexploitation, particularly in mobile or migratory species (Hannesson 1998; Hilborn et al. 2004; Kaiser 2005). As many commercially harvested species undergo seasonal migrations or are highly mobile, this possibility deserves careful consideration. Indeed, most documented cases of fisheries benefits derived from the implementation of a marine reserve are for coral-reef species, which have a more localized home range (Halpern and Warner 2002; Halpern 2003). However, even though reserves may be less effective for highly mobile species (Kramer and Chapman 1999; Botsford et al. 2001; Gerber et al. 2005), they may still offer much needed protection of life stages or locations that are particularly vulnerable to harvest (Gell and Roberts 2003; Roberts et al. 2005).

Migratory species give rise to additional complications when considering the effectiveness of reserves for reducing undesirable effects of fisheries-induced evolution. In particular, for the many commercially important fish stocks that undergo an annual migration between feeding grounds and spawning grounds (including many pelagic species such as tunas and clupeoids, and demersal species such as Atlantic cod and plaice), the selective pressures imposed by fishing can vary considerably depending on where fishing takes place. Fishing in the feeding grounds can be expected to cause evolution of earlier maturation, if both juveniles and adults are captured (Law and Grey 1989; Heino et al. 2002b; Heino and Godø 2002). In contrast, fishing in the spawning grounds favors individuals that delay maturation until they are larger and more fecund (Law and Grey 1989; Heino and Godø 2002). From a combined evolutionary and management perspective, fishing in the feeding grounds results in possibly undesirable consequences, because individuals allocate energy away from growth and toward reproduction earlier in life, potentially altering biomass and yield (Law and Grey 1989). A marine reserve could have very different effects depending on whether it is located in feeding or spawning grounds (Law 2007). In such cases, the ideal placement and effects of a marine reserve are not straightforward. Protection on the feeding grounds might dilute some of the benefits of implementing a marine reserve, because adults might fully mix in the spawning grounds. Conversely, protection on the spawning grounds might exacerbate evolution of earlier maturation caused by a feeding-ground fishery because individuals may gain higher fitness from maturing early to seek protection on the spawning grounds (Law 2007). So far, it is also unclear how soon after a reserve's establishment potentially mitigating evolutionary consequences might take effect, and how trade-offs between short-term and long-term reserve effects might complicate the evaluation of management strategies.

In this study, we present an eco-genetic model (e.g., Dunlop et al. 2007; Thériault et al. 2008; Dunlop et al. 2009; Enberg et al. this issue; Okamoto et al. this issue; Wang and Höök this issue) to explore the effects of marine reserves on the evolutionary response to fishing in a migratory species. Our model is motivated by the life history of Atlantic cod (*Gadus morhua*).

Many northern populations of Atlantic cod, most notably Northeast Arctic cod off northern Norway and Icelandic cod on the Icelandic Shelf, display a far-ranging annual migration between spawning and feeding grounds (Robichaud and Rose 2001; Godø 2003; Palsson and Thorsteinsson 2003; Robichaud and Rose 2004). Northern populations of cod also share other life-history characteristics such as relatively slow growth to potentially large body size and relatively late maturation at large size. Moreover, cod is among the most valuable fishery targets in the North Atlantic, and there is evidence suggesting that significant fisheries-induced evolution has already occurred in many cod populations (Heino et al. 2002b; Barot et al. 2004; Olsen et al. 2004; Olsen et al. 2005; Swain et al. 2007, 2008). Here we do not aim at precisely modeling any particular cod population, but instead develop and analyze a model representing life history of cod in the northern parts of its range, as an example of a commercially exploited, long-lived, migratory fish.

The model developed here extends previous marine-reserve models (e.g., Guenette and Pitcher 1999; Baskett et al. 2005; Hart 2006; Miethe et al. 2009) by (i) considering the evolution of multiple life-history traits (for growth, maturation schedule, and reproductive investment), (ii) accounting for density dependence in growth and reproduction, and (iii) examining a migratory life history. The inclusion of density-dependent somatic growth is a particularly relevant extension, because it is known to play a critical role in determining the effectiveness of a reserve under conditions of crowding (Gårdmark et al. 2006).

Below, we first present an eco-genetic model for a migratory population harvested on spawning and feeding grounds. We then investigate scenarios in which a marine reserve is established either on the stock's spawning grounds or on its feeding grounds, by comparing life-history evolution, total catch, and fish size in the catch. Finally, we assess the sensitivity of our findings to assumptions about movement rates, presence or absence of natal homing or spawning migration, and displacement of fishing effort. Our results suggest that a reserve located on a stock's feeding grounds could mitigate fisheries-induced evolution, but that beneficial effects on yield can only be expected long after the reserve's establishment.

Methods

We constructed an individual-based eco-genetic model (for a description of eco-genetic models see Dunlop et al. 2009) to follow the evolution of four quantitative life-history traits: growth capacity, reproductive investment, and the intercept and slope of a linear probabilistic maturation reaction norm (PMRN; described in more detail below). The core of the model is the same as the example in Dunlop et al. (2009) except with a spatial dimension and annual migration added. Events in our model occur in discrete annual time steps. In each time step, individuals can mature, grow, migrate, reproduce, and experience natural and fishing mortality, in this order (Fig. 1). For each individual, we follow its location (reserve or harvested area), size and age, and maturation status in time. We run the model for 2000 yrs prior to harvest, to ensure that population abundance and evolving traits have reached a stochastic equilibrium. We parameterize the model based on Atlantic cod *Gadus morhua* (see Table 1 for parameter values and justifications) for three reasons: (i) Atlantic cod is one of the commercially most important fish species worldwide, (ii) several stocks of this species undergo substantial annual spawning migrations (Rose 1993; Jonsdottir et al. 1999; Comeau et al. 2002; Godø 2003), and (iii) several stocks have shown evidence of fisheries-induced evolution in maturation schedules and length-at-age (Heino et al. 2002b; Barot et al. 2004; Olsen et al. 2004, 2005; Swain et al. 2007, 2008). Parameter values were obtained from published data and were characteristic for Atlantic cod in the northern part of its range, such as Icelandic cod, Northeast Arctic cod off Norway, and northern cod off the east coast of Canada (Table 1). No one stock contained all parameter values and so we had to rely on multiple sources of data.

Reserve design

All protected areas in the model are no-take reserves. At the time of reserve implementation, all individuals in the population are assumed to be randomly distributed in space. The reserve is then implemented by designating a proportion $A_{L,\mathrm{R}}$ of the total area occupied by the population as no-take, where the location index $L = \mathrm{F}$ stands for a feeding-ground reserve and $L = \mathrm{S}$ for a spawning-ground reserve. For comparison, we also model populations with no separate feeding and spawning grounds, to test whether their distinction alters the effectiveness of the reserve.

We examined the effectiveness of each reserve location in two different reserve-establishment scenarios. In the first scenario, the reserve is established when fishing begins. This allows evaluation of the capacity of reserves to prevent fisheries-induced evolution from occurring in the first place. In the second scenario, fishing occurs for 50 years before the reserve is established. This allows examination of the propensity of reserves to slow, stop, or reverse fisheries-induced evolution once such evolution is already underway. For all scenarios, we investigated several different relative reserve sizes $A_{L,\mathrm{R}}$ between 0 (no reserve) and 1 (entire area is protected).

Movement

All individuals have an annual probability of moving between the reserve and the harvested area. The conditional probability of movement is a function of the proportion $A_{L,\mathrm{R}}$ of the total area in the reserve or the proportion $A_{L,\mathrm{H}} = 1 - A_{L,\mathrm{R}}$ in the harvested area. The conditional movement probability also depends on the reserve's retention probability q, such that a proportion q of individuals remain within the reserve, while the remaining proportion $1-q$ disperse globally, and therefore are equally likely to end up in the reserve R or in the harvested area H in strict proportion to their relative areas. Hence, the probabilities of remaining in an area and of moving, conditional upon the current location, are given by

$$P_{L,\mathrm{R|R}} = q + (1-q)A_{L,\mathrm{R}}\,, \tag{1a}$$

$$P_{L,\mathrm{H|H}} = q + (1-q)A_{L,\mathrm{H}}\,, \tag{1b}$$

$$P_{L,\mathrm{H|R}} = (1-q)A_{L,\mathrm{H}} \tag{1c}$$

$$P_{L,\mathrm{R|H}} = (1-q)A_{L,\mathrm{R}} \tag{1d}$$

where $L = \mathrm{F}$ refers to fish in the feeding grounds and $L = \mathrm{S}$ to fish in the spawning grounds. The amount of movement is likely to influence the efficacy of the reserve (Baskett et al. 2005) and we therefore vary q to test the influence of retention probability on model predictions.

Genetic structure

The genetic component of the model describes (i) the distribution of the evolving genetic traits in the initial population, (ii) inheritance of genetic traits from parents to offspring, and (iii) inter-individual environmental variation to determine the phenotypic expression of genetic traits. We use quantitative genetics to describe changes in trait values (Falconer and Mackay 1996).

Following this framework, values for each of the four evolving traits (growth capacity, reproductive investment, and the intercept and slope of a linear probabilistic maturation reaction norm, PMRN) are assigned to individuals in the initial population based on a normal distribution with a mean $\overline{x}$ given by empirical data and a genetic standard deviation $\sigma_{\mathrm{G},x}$ calculated from an assumed coefficient of genetic variation $C_\mathrm{G} = \sigma_{\mathrm{G},x} / \overline{x}_\mathrm{G}$ (Houle 1992), where x_G indicates the value of the genetic trait in question ($x_\mathrm{G} = i_\mathrm{G}$ for the PMRN intercept, $x_\mathrm{G} = s_\mathrm{G}$ for the PMRN slope, $x_\mathrm{G} = g_\mathrm{G}$ for growth capacity, and $x_\mathrm{G} = r_\mathrm{G}$ for reproductive investment). Offspring inherit the genetic trait values of their parents from a normal distribution with a mean equal to the mid-parental value and a variance equal to half the genetic variance in the initial population (thus assuming a constant mutation-recombination-segregation kernel; see Roughgarden 1979; Dunlop et al. 2009b). All genetic traits evolve independently in this model, and we thus ignore any possible pleiotropy or genetic linkage between traits.

The phenotypic expression of any genetic trait x_{G} occurs annually by drawing phenotypic trait values x_{P} from a normal distribution with mean x_{G} and inter-individual environmental variance $\sigma_{\mathrm{E},x}^2$. The latter is parsimoniously held constant through time and is calculated as $\sigma_{\mathrm{E},x}^2 = \sigma_{\mathrm{G},x}^2(1/h_{x,0}^2 - 1)$, where $\sigma_{\mathrm{G},x}^2$ is the initial genetic variance of trait x_{G} and $h_{x,0}^2$ is the assumed heritability of x_{G} in the initial population (Falconer and Mackay 1996). Therefore, each genetic trait value x_{G} has a corresponding phenotypic trait value x_{P}.

Maturation

We include phenotypic plasticity in the maturation process by modeling probabilistic maturation reaction norms (Heino et al. 2002a; Dieckmann and Heino 2007). Each individual is characterized by a PMRN that represents it genetic predisposition to mature as a function of age and size. In our model, two traits describe the PMRN: its slope and intercept. The slope is a measure of the degree of phenotypic plasticity in maturation: a slope of zero (i.e., a completely horizontal PMRN) indicates that there is phenotypic plasticity in age at maturation but not in size at maturation, whereas a slope approaching infinity (i.e., a completely vertical PMRN) indicates phenotypic plasticity in size at maturation but not in age at maturation. Together, the PMRN intercept and PMRN slope influence the sizes at which maturation occurs for any particular age.

Each year, the probability p_{m} of an immature individual to mature is a function of its age a and body length l_a,

$$p_{\mathrm{m}}(a,l) = [1 + \exp(-(l_a - l_{\mathrm{p50},a}) / z)]^{-1}, \tag{2a}$$

where $l_{\mathrm{p50},a}$ denotes the length at 50% maturation probability at age a (also known as the PMRN midpoint at age a) and is determined by an individual's phenotypic values for the PMRN slope s_{P} and intercept i_{P},

$$l_{\mathrm{p50},a} = s_{\mathrm{P}} a + i_{\mathrm{P}}. \tag{2b}$$

The parameter that controls how the maturation probability p_{m} at age a changes with the difference between the length l_a and $l_{\mathrm{p50},a}$,

$$z = w / \ln \frac{p_{\mathrm{l}}^{-1} - 1}{p_{\mathrm{u}}^{-1} - 1}, \tag{2c}$$

is described by the PMRN width w, which measures the length difference at age a over which the maturation probability p_{m} increases from p_{l} to p_{u} (Heino et al. 2002a). The two latter probabilities define the upper and lower bounds of what is called the maturation envelope (represented in our model by quartiles, $p_{\mathrm{l}} = 25\%$ and $p_{\mathrm{u}} = 75\%$). The PMRN width is assumed to be independent of age and constant in time. This latter assumption is underpinned by the prior investigation of models in which w was incorporated as an additional evolving trait, which showed that selective pressures on, and resultant evolutionary changes in, w were minimal.

Somatic growth

The somatic growth of individuals depends on multiple factors: (i) the individual's growth capacity phenotype, i.e., the maximum possible growth in the absence of density dependence, but including inter-individual environmental variation; (ii) population biomass, owing to density dependence in growth; (iii) inter-annual and inter-individual environmental variance in growth capacity; and, after maturation, on (iv) the individual's reproductive investment phenotype. In our model, growth takes place in the feeding area and, for a given individual, therefore depends on the density of fish residing at the individual's location in the feeding area. This density naturally differs between the reserve and the harvested area, yielding an annual amount of energy available for growth of

$$g_{\mathrm{d},X} = \frac{g_{\mathrm{P}}}{1 + (bB_{\mathrm{F},X} / A_{\mathrm{F},X})^{c}}, \tag{3a}$$

where b and c are constants, g_{P} is the phenotypic growth capacity, $B_{\mathrm{F},X}$ and $A_{\mathrm{F},X}$ are the biomass in, and proportional area of, respectively, the feeding area in which the individual is located ($X = \mathrm{R}$ for the feeding-ground reserve or $X = \mathrm{H}$ for the feeding-ground harvested area).

Immature individuals invest all available energy into growth, growing from length l_a at age a to length l_{a+1} at age $a+1$ (Lester et al. 2004),

$$l_{a+1} = l_a + g_{\mathrm{d},X}, \tag{3b}$$

with $l_0 = 0$. Mature individuals, in contrast, partially utilize energy for reproduction that would have gone solely into the growth increment $g_{\mathrm{d},X}$ (Lester et al. 2004),

$$l_{a+1} = \frac{3}{3 + \delta r_{\mathrm{P}}}(l_a + g_{\mathrm{d,X}}), \tag{3c}$$

where r_{P} is the phenotypic reproductive investment, measured as the gonado-somatic index (GSI; the ratio of gonad mass to somatic mass), and δ is a conversion factor that accounts for the higher energy content of gonads relative to somatic tissue (Lester et al. 2004). If the r_{P} of an individual in a given year would cause negative growth ($l_{a+1} < l_a$), r_P for that year is reduced such that l_{a+1} equals l_a.

Reproduction

After the growing season, mature individuals migrate to the spawning grounds to reproduce. Following a common observation in many fish species (Kjesbu et al. 1998; Lloret and Ratz 2000; Oskarsson et al. 2002; Kennedy et al. 2007), gonad mass $m_{\mathrm{G},a}$ at age a, and therefore fecundity at that age, increase allometrically with body length, based on a proportionality constant α and an allometric exponent β,

$$m_{\mathrm{G},a} = \alpha l_a^\beta r_\mathrm{P}, \tag{4a}$$

where r_P is the individual's phenotypic reproductive investment, as measured by its gonado-somatic index (GSI). The fecundity of each female is then equal to $f = d m_{\mathrm{G},a}$, where d is the weight-specific oocyte density. The number N_r of surviving offspring (i.e., recruits) produced by the population is determined by a Beverton-Holt stock-recruitment function (Hilborn and Walters 1992),

$$N_\mathrm{r} = \frac{k f_\mathrm{T}}{1 + f_\mathrm{T} / j}, \tag{4b}$$

where the total fecundity f_T is obtained from summing fecundity over all mature females, k is the density-independent survival probability of offspring, and j is the total fecundity at which offspring survival is reduced by 50%.

Within a particular spawning area (reserve or harvested area in model designs with a spawning-ground reserve), males and females encounter, and mate with each other at random, with the number of resultant offspring being proportional to each parent's gonad mass. We take this approach because individuals with large gonads are expected to possess larger numbers of gametes (eggs or sperm) and therefore will have a larger number of offspring. Also, a given female could mate with several males and a given male could mate with several females, in accordance with expectations for a batch-spawning species such as Atlantic cod (McEvoy and McEvoy 1992).

The probabilities of newly born offspring and first-time spawners to end up growing and feeding in the reserve or the harvested area equal their relative areas, $A_{\mathrm{F,R}}$ and $A_{\mathrm{F,H}}$, in those locations. This assumes that individuals choose their initial feeding and spawning site randomly.

Natal homing

Our default models assume feeding-site and spawning-site fidelity, but no natal homing. We also considered an alternative model with natal homing because (i) there is evidence that many marine species have spatially or genetically distinct local sub-populations (Hutchinson et al. 2001; Conover et al. 2006; Pampoulie et al. 2006), (ii) there is evidence for natal homing and spawning-site fidelity in cod and other species (Robichaud and Rose 2001; Thorrold et al. 2001; Hunter et al. 2003; Svedang et al. 2007), and (iii) natal homing could be particularly important when designing or implementing spawning-ground reserves (Almany et al. 2007). Further methodological details are provided in Appendix A.

Natural mortality

In addition to the offspring mortality described by the stock-recruitment relationship above, a classic growth-survival tradeoff is assumed (Stearns 1992), causing a post-recruitment density-independent mortality probability of

$$p_{\mathrm{G}} = g_{\mathrm{G}} / g_{\max}, \tag{5a}$$

where g_{G} is the genetic growth capacity and $g_{\max}$ is the maximum annual length increment at which the survival probability drops to 0. The growth survival tradeoff assumes that individuals that have a high genetic propensity for growth, independent of the environment, have a higher mortality rate. We also impose a constant annual mortality probability p_{B} on all individuals, so that the total natural mortality probability p_{T} equals that used by ICES (2007) in their stock assessment of Atlantic cod, i.e., $p_{\mathrm{B}} = 1-(1-p_{\mathrm{T}})/(1-p_{\mathrm{G}})$. Mortality probabilities in the model are implemented by drawing a random number between 0 and 1; if that number is less than the mortality probability, the individual dies and is removed from the population.

Fishing mortality

Fishing occurs during the growing season on the feeding grounds and during the spawning season on the spawning grounds (e.g., Godø 2003). The fishery is regulated through an annually set total allowable catch $B_{\mathrm{TAC},t}$, which is determined by the product of the harvest ratio γ and the total harvestable biomass, defined as the total biomass of individuals in the population with lengths greater than the minimum size limit l_L of the fishery,

$$B_{\mathrm{TAC},t} = \gamma(H_{\mathrm{F},t} + H_{\mathrm{S},t}), \tag{6a}$$

where $H_{\mathrm{F},t}$ and $H_{\mathrm{S},t}$ are, respectively, the harvestable biomass in the feeding and spawning grounds. We employed a management regime that takes into account the potential displacement of effort by a marine reserve, implying that harvest probability for individuals outside a reserve become elevated in response to reserve establishment (e.g., Hilborn et al. 2006). As all mature individuals are considered to be fully recruited to fishing gear in many fisheries, in our model all mature fish on the spawning grounds are vulnerable to harvest and there is no minimum-size limit there ($l_{\mathrm{S}} = 0$). We also consider a fishery in which the displacement of effort does not occur and the total allowable catch therefore is given by the proportion of the harvestable biomass in the harvested area only (i.e., excluding the harvestable biomass in the reserve). To calculate biomass, the length of individuals is converted to weight by raising length to an allometric exponent β and multiplying by a proportionality constant α.

The total allowable catch is then divided between catch in the spawning grounds ($B_{\mathrm{S},t}$) and catch in the feeding grounds ($B_{\mathrm{F},t}$). In each location, individuals in the harvested area that are larger than l_L are randomly harvested until that area's allowable catch has been reached. We analyzed several different ratios $R_\mathrm{F} : (1 - R_\mathrm{F})$ between feeding-ground catch and spawning-ground catch,

$$B_{\mathrm{F},t} = R_\mathrm{F} B_{\mathrm{TAC},t} \text{ and } B_{\mathrm{S},t} = (1 - R_\mathrm{F}) B_{\mathrm{TAC},t}, \tag{6b}$$

where R_F is the proportion of the total catch that is allocated to the feeding grounds. The cumulative catch that we report in the results is calculated as the total biomass of fish captured and killed in the fishery, measured over the 100 years during which fishing occurs. The annual yield or catch is the biomass of fish captured and killed by the fishery for a given year.

Results

We start by establishing a baseline through investigating fisheries-induced evolution in the absence of a reserve. We then study the effects of reserves on evolutionary changes and on cumulative catches, before examining the effects of mobility and the annual spawning migration. Finally, we evaluate the expected impacts of reserves that are established only after a longer period of fishing.

Evolutionary response to fishing in the absence of reserves

To determine the evolutionary effects of fishing in our model, we first explore outcomes without reserves. In absence of a reserve (Fig. 2, results on the y-axes), taking an increasing fraction of total catch in the feeding grounds relative to the spawning grounds (i.e., increasing R_F) causes the PMRN midpoint (Fig. 2a) and growth capacity (Fig. 2c) to decline and the gonado-somatic index to increase (Fig. 2e). Relative to pre-fishing trait values (dashed lines), reproductive investment always increases when the stock is adapting to fishing, but maturation and growth may either increase or decrease, depending on where the larger part of catches are taken. If most of the catches are taken in the spawning grounds, no maturation evolution occurs relative to pre-fishing equilibrium, but growth is still evolving. Similarly, one could choose to split the catches such that no growth evolution would occur.

Influence of reserves on fisheries-induced evolutionary changes

Next, we assess how evolutionary outcomes depend on reserve placement in feeding or spawning grounds. The creation of a spawning-ground reserve has an overall small impact on the amount of evolution relative to when the reserve area is 0 (Fig. 2a,c,e), while protecting spawning grounds can have a large influence on the amount of evolution (Fig. 2b,d,f). Not surprisingly, the influence of a spawning or feeding ground reserve is greatest when most fishing takes place in the spawning or feedings ground, respectively. The influence of a reserve on maturation evolution is qualitative different between feeding and spawning grounds: a reserve in the feeding grounds favors delayed maturation (Fig. 2b), whereas a reserve in the spawning grounds favors earlier maturation (Fig. 2a). Similar pattern applies to evolution of growth (Fig. 2c,d), but not reproductive investment that declines with increasing reserve area both for spawning and feeding grounds reserves (Fig. 2e,f). Thus, for maturation and growth the impact of creating a feeding ground reserve is the same as taking a larger proportion of catch in the spawning grounds, and the impact of creating a spawning ground reserve is the same as taking a larger proportion of catch in the feeding grounds. In this sense, the spawning-ground reserve can be thought of as exacerbating the evolution towards earlier maturation and slower growth caused by fishing in the feeding grounds.

We do not show results for the evolution of the PMRN slope because almost all of the evolutionary change in the PMRN is caused by evolution of the PMRN intercept: for example, fishing solely in the feeding grounds causes a large decrease in the PMRN intercept of 34% combined with only a slight increase in the PMRN slope of 0.23%, with both changes expressed relative to the year before fishing (see also Dunlop et al. 2009). Genetic variances were found to be little influenced by fishing and therefore, not surprisingly, by the creation of a marine reserve (results not shown). The variation between model runs was relatively small (for example in the year just prior to fishing the mean and standard deviation of the PMRN intercept was 90.4 and 1.1 cm, respectively).

Influence of reserves on yields

To determine the effects of evolutionary changes and of reserves on cumulative catches, we investigate catches resulting under the different scenarios. Reserves alter the cumulative catch of the fishery (Fig. 3), as is apparent by comparing simulations without a reserve (i.e., results on the y-axes) to those with a reserve. In most cases, increasing reserve in one area diminishes catches in that area (Fig. 3a,d) but improves the catches in the other area (Fig. 3b,c); in most cases the total catch is decreased because the loss in one area is imperfectly compensated by the gain in the other area. The influence of a spawning ground reserve on catch close to linear (Fig. 3a,c), whereas the influence of a feeding ground reserve becomes only apparent above a certain threshold (Fig. 3b,d); below this threshold, the reserve may slightly improve the total catch when all fishing is in the feeding grounds (R_F =1). Feeding ground reserves often improve catch in terms of mean length of fish in the catch. However, small spawning ground reserves actually results in a lower mean length.

Effects of mobility

To determine the influence on our results of the movement of fish among areas, we tested the sensitivity of our model results to the level of mobility, by changing the retention probability q : decreasing q results in an increase in the movement between reserves and harvested areas. We find that greater individual movement lessens the effectiveness of a feeding-ground reserve in reducing fisheries-induced evolution (Fig. 4a,b,c). As there is little effect of a spawning-ground reserve on trait evolution, there also is little influence of mobility on the effectiveness of a spawning-ground reserve (Appendix A). Similar effects of movement were noted in populations with natal homing (Appendix A), indicating that natal homing had virtually no impact on the predictions of our model.

Effects of annual spawning migration

To quantify the effects of an annual migration between feeding and spawning grounds, we compared results to a scenario in which the annual spawning migration was switched off (Appendix B). In the absence of a reserve, a non-migratory population responds to fishing similarly to a migratory population harvested only on its feeding grounds, but the evolutionary response is less pronounced (Fig. B1). When a reserve is implemented, the evolutionary response of this population is almost indistinguishable from that of a migratory population with a feeding-ground reserve. On the other hand, the evolutionary response of a migratory population harvested on its spawning grounds differs starkly from that of a non-migratory population, unless a large part of either population is protected by a reserve (Appendix B).

Effects of creating a reserve only after 50 years of fishing

In the investigations above, we implemented fishing and reserves simultaneously to explore the potential for reserves to reduce fisheries-induced selection. In a final step, we explore the potential for, and timescale of, fisheries-induced evolution to be reversed through reserve establishment. If 50 years of fishing pass by before a reserve is implemented, its effectiveness in slowing down evolution depends on harvest probability and reserve area (Fig. 5a,c,e). Populations that are fished more intensively show the largest reduction in the rate of evolution when a feeding-ground reserve is implemented (Fig. 5e), whereas implementing a small reserve for a lightly fished population has hardly any noticeable effect on the rate of evolution (Fig. 5a, thin line). The creation of a reserve always causes an initial reduction in annual yield, which may be followed by a short-term recovery in yield when the population approaches its new demographic equilibrium (Fig. 5b,d,f). On longer time scales, we see that fisheries-induced evolution continues despite a reserve, but also that the quantitative difference between the magnitudes of evolution in a protected and a non-protected population increases for a long period of time (Fig. 6a). More importantly, after a while, the annual yield that can be extracted from a population protected by a reserve will be higher than if no reserve were created (Fig. 6b).

Discussion

The central goal of this study was to evaluate the effectiveness of marine reserves in reducing the evolutionary effects of fishing in a species undergoing an annual spawning migration. The model presented here suggests that the selective pressures caused by fishing in a stock's feeding grounds are, for the most part, different than the selective pressures caused by fishing in the spawning grounds. This finding of differential selective pressures is in accordance with earlier studies relying on simpler models (Law and Grey 1989). We extend earlier analyses by considering the effects of reserve placement on fisheries-induced evolution in a migrating population and by incorporating density-dependent growth and the evolution of life-history traits beyond those affecting maturation. Some other novel features of our approach are discussed under the heading 'Eco-genetic modeling' below.

Effects of spatial stock structure

The reason for the selective pressures in our model to differ qualitatively between spawning grounds and feeding grounds is that when fishing occurs in the latter, both juveniles and adults are subject to being harvested above a minimum-size limit, so that evolution favors fish that mature earlier, have slower growth, and invest a higher proportion of energy in reproduction (Fig. 2, $R_F = 1$). In contrast, when fishing occurs in the spawning grounds, only adults are harvested, so that individuals maturing later, when they are larger and more fecund, experience a higher reproductive success (Fig. 2a,b, $R_F = 0$). Fast growth rates (Fig. 2c,d, $R_F = 0$) and a higher investment in reproduction (Fig. 2e,f, $R_F = 0$) are also favored by fishing in the spawning grounds.

It is interesting to note that adding a conservative minimum size limit to the spawning ground fishery could also favor early maturation (Jørgensen et al. 2009). In our model, we chose not to implement such a minimum-size limit on the spawning grounds, because mature size classes are often fully recruited to fisheries. Also, spawning ground fisheries often tend to be coastal, using more traditional methods (e.g., hand lines from smaller boats versus trawling from open-ocean vessels) that are less selective for size; this is the case, for example, for the spawning-ground fishery for Northeast arctic cod off Norway (Godø 2003).

Owing to the spatially distinct selective pressures, the success of marine reserves in reducing fisheries-based evolutionary change is contingent upon the location of the reserve. The implementation of a marine reserve in the feeding area can have significant effects by protecting individuals before reproduction: the evolutionary response to fishing in the modeled life-history traits diminishes as the area of the reserve increases (Fig. 2b,d,f). However, the propensity of a marine reserve to reduce evolution is lessened when the reserve is located on the spawning grounds (Fig. 2a,c,e). As fishing in the feeding grounds causes the largest evolutionary change, a spawning ground reserve can do little to curb these effects. Furthermore, by protecting spawning individuals that would have been harvested, selection favoring delayed maturation and faster growth is lessened. In other words, we see that a spawning ground reserve can enhance the evolutionary response towards earlier maturation and slower growth that is induced by fishing in the feeding grounds (Fig. 2). Therefore, if the management goal is to reduce the amount of fisheries-based evolution, the optimal location for a reserve is in a population's feeding grounds.

Effects of reserve size

The size of a reserve that is most effective in reducing fisheries-induced evolution depends on the ratio between feeding-ground catch and spawning-ground catch, as well as on the mobility of individuals (Fig. 2 and 4). When the total allowable catch in the feeding grounds is high, even a smaller reserve can offer benefits in terms of reducing the magnitude of evolutionary changes. In contrast, if fishing pressure in the spawning grounds is higher, only the very largest reserves are effective (Fig. 2; Appendix A) and there is so little fisheries-induced selection that it is perhaps not worthwhile to implement a reserve if its only goal is to prevent fisheries-induced evolution. We also see that as the mobility of individuals in the population is increased, the reserve needs to be increasingly larger in order to lessen evolution (Fig. 4); these results are related to arguments that reserves will be less effective or need to be extremely large for mobile species (Hannesson 1998; Hilborn et al. 2004). Furthermore, when harvest pressure is low, the reserve needs to be slightly larger when there is an annual migration between spawning and feeding grounds; this is because of the gene flow that occurs between individuals while they reside on the spawning grounds (Appendix B). The results of our study underscore the idea that taking into account the selective pressures of fishing in different locations and the patterns of movement of species among those locations is crucial when assessing implementation options for marine reserves.

Effects of a reserve on yield

Although our model suggests that a feeding-ground reserve can reduce the magnitude of fisheries-induced evolution, such a reserve has more complex effects on catch. The creation of a reserve almost always caused a reduction in cumulative catch (Fig. 3-6). Yield increases were only noted for a few scenarios and tended to be small in magnitude. First, when a reserve was created and fishing started simultaneously, slight increases in cumulative catch (over 100 years) were observed when all fishing pressure was concentrated in the feeding grounds (Fig. 3); these increases were most obvious when movement rates between the reserve and harvested areas were higher (Fig. 4). Second, creating a feeding-grounds reserve enhanced catches in the spawning grounds, and creating a spawning-ground reserve could improve catches in the feeding grounds (Fig. 3). These effects are a consequence of changes that are in part demographic and in part to evolutionary. Protecting fish in the feeding grounds can enable the rebuilding of size structure in the population, whereas protecting spawning individuals can enhance offspring production. Third, when a feeding-ground reserve was fishing created after 50 years of fishing, there was always an initial reduction in yield (Fig. 5), but after some time, which in our example ranged from about 50 to several hundreds of years, yield could be enhanced relative to a population that was not protected (Fig. 6). The increases in catch that were observed in the three situations described above are probably not substantial enough to warrant creating a reserve solely based on the goal of enhancing yield.

Our results show that marine reserves can help to mitigate fisheries-induced evolution, but that this mostly implies reduced yield, especially in the short to medium term. Motivated by the discussion about fisheries benefits of marine reserves (Hannesson 1998; Hastings and Botsford 1999; Hilborn et al. 2004), one could ask whether the same benefits could have been achieved by simply reducing the harvest ratio, without implementing a reserve. Our results confirm that reducing harvest rates can considerably lessen the magnitude of fisheries-induced evolution (as shown in Fig. 5, as well as Appendices B and C; see also Law and Grey 1989; Heino 1998; Ernande et al. 2004; Dunlop et al. 2009). As an option for future research, it will therefore be interesting to compare in detail the costs and benefits associated with the two alternative management strategies, of reducing harvest ratio and reducing harvest area, to establish whether, taking fisheries-induced evolution into account, reserves can offer a better benefit-to-cost ratio than traditional management strategies.

Other reserve benefits

There could be fisheries benefits to slowing down or reducing the magnitude of fisheries-induced evolution other than those accruing in the form of enhanced yields (e.g., Kirkpatrick 1993; Baskett et al. 2005). For example, fisheries-induced evolution can lead to reduced body sizes in the catch, a trend that can be alleviated through creating a feeding-ground reserve (Fig. 3). Also, there is some indication from our results that the creation of a reserve could improve yield stability: Fig. 5 shows that there is a steady reduction in yield in response to fishing, but that, after the strong initial decrease, the creation of a feeding-ground reserve can substantially slow the decline. Finally, evolution could have other effects, possibly altering species interactions, recovery potential, and migration patterns (Gårdmark et al. 2003; Jørgensen et al. 2007, 2008a; Thériault et al. 2008; Jørgensen et al.; Enberg et al. 2009). Protected areas could offer management options for mitigating such other effects, as our results show that feeding-ground reserves are capable of reducing the magnitude of evolutionary changes caused by fishing.

Effort displacement

The impact of effort re-allocation should be considered when designing a marine reserve (Hilborn et al. 2004). Our model can account for the often high harvest pressure that develops in areas outside the reserve, because the harvest ratio in our model is expressed as a proportion of the population's total harvestable biomass, which includes the biomass of individuals residing both inside and outside the reserve. Therefore, a build-up of biomass in the reserve while the harvest ratio is kept constant results in higher harvest probabilities per individual outside of the reserve. We find that even with such a harvesting pattern reflecting effort displacement in the wake of reserve's creation, feeding-ground reserves can reduce evolution and sometimes enhance yield. When creating a feeding-ground reserve, excluding effort displacement by setting the harvest ratio to be a proportion of the harvestable biomass in the harvested area only (thus, not including the biomass inside the reserve), results in a slight reduction of fisheries-induced evolution, but only for low harvest ratios and reserves of small to medium size (Appendix C). These results agree with findings by Baskett et al. (2005), who predicted that sufficiently large reserves may protect against strong fisheries-induced selection for earlier maturation irrespective of whether or not harvest rates outside of the reserve were increased through effort displacement.

Eco-genetic modeling

The model used here for analyzing the evolutionary effects of marine reserves in migratory stocks builds upon previous eco-genetic models (Dunlop et al. 2007, 2009b). Our model permits the examination of multi-trait evolution and of density-dependent growth, features not included in previous marine-reserve models. We can also study evolutionary transients, something not possible with many other types of models, such as optimization models or adaptive dynamics models. Full integration of ecological and evolutionary timescales, as offered by eco-genetic modeling, is important in studies of marine reserves, as where short-, medium-, and long-term consequences need to be properly balanced and evaluated. In our results, implementing a marine reserve always caused an initial reduction in yield, even though, as evolutionary effects emerge over time, the reserve could enhance yield (Fig. 6). By examining the transients in Figs. 5 and 6, e can discern three stages of this process. First is the immediate drop in yield that occurs with the displacement of effort. Second is the arched increase in yield that occurs approximately 55-70 years after the reserve establishment, as biomass accumulates in the reserve and the stock's age and size structure build up. This second stage could be interpreted as an ecological response (Gaylord et al. 2005). Third is the long-term trend in yield that results from the evolutionary response. Without a simultaneous treatment of ecological and evolutionary timescales, these dynamics could not be discerned and examined.

Generalizations to other species

Our modeled population most closely resembles Atlantic cod stocks found in the northern part of the species range, including Icelandic cod, Northeast Arctic cod off Norway, or northern cod off the east coast of Canada. We focus on Atlantic cod because data are available to parameterize the model, the species is of considerable commercial and ecological importance, exploitation rates are often high, and many stocks of Atlantic cod undergo long spawning migrations resulting in the geographical separation of feeding and spawning grounds (Robichaud and Rose 2004). The parameter values we chose are validated in the sense that they result in emergent properties, including growth patterns and other life-history observables, that are very similar for northern populations of Atlantic cod (see Table 1). In this sense, our study conforms to the pattern-oriented modeling approach described by Grimm and Railsback (2005). Although we have not explored the effects of exploitation and marine reserves on species with other life histories, one simple generalization can be drawn. Our modeled cod population had a moderately high age at maturation of 8 years in the absence of fishing. Species or populations with shorter generation times – such as cod in the southern parts of its range, and several key commercial targets such as herrings and flatfishes – will probably show faster evolutionary responses. As the evolutionary effects will then accrue more quickly, the benefits of implementing a reserve might also be observed on a shorter timescale. However, much more investigation is needed to determine the quantitative influence of life history on the combined effects of fisheries-induced evolution and marine-reserve implementation. We contend that the results reported here should foster the understanding that evolutionary impacts of marine reserves be assessed through the calibration of stock-specific models, before managers and stakeholders commit to costly implementation measures. For this, the framework laid out here can provide a template.

Model uncertainty

There is little data evidence with which to compare the predictions of our model. This is because the majority of previous studies have focused on the ecological effects of reserves, or examined timescales too short for evaluating evolutionary impacts. Some empirical evidence shows that increases in biomass and species diversity in marine reserves can be observed very quickly, with the potential for spillover to areas outside reserves, thereby suggesting that there could be significant demographic, nonevolutionary impacts (e.g., Roberts et al. 2001; Halpern and Warner 2002). However, evolutionary effects are slower and will take longer to observe, which obviously poses a challenge when trying to evaluate the efficacy of reserves to reduce the magnitude of fisheries-induced evolution. There is one study that does point to the possible genetic effects of marine reserves. Perez-Ruzafa et al. (2006) found higher intra-specific allelic diversity for sea bream inside two Mediterranean reserves than in neighbouring nonprotected areas. At the time of sampling, the reserves were protected for 4 and 10 years. Although no data on life-history traits were reported, Perez-Ruzafa et al. (2006) suggest that the preservation of individuals with higher fecundity and faster growth reduced selective pressures induced by fishing, a mechanism that could have increased allelic diversity in the reserve.

While the numerical approach here limits our analysis to the parameter values used, in this study we tested the sensitivity of our predictions to several parameters, including retention probability, reserve area, harvest rate, time of reserve implementation, and the presence of natal homing. In another study (Dunlop et al. 2009b) the sensitivity of the base model was tested to changes in harvest rate, the minimum-size limit, the stock-recruitment relationship, density-dependent growth, genetic variation, and the growth-survival trade-off; that sensitivity analysis revealed that the speed of evolution depends on these functions, supporting their presence in the models, but the overall qualitative effects of exploitation remained the same: fishing caused most evolution in the PMRN toward earlier ages and smaller sizes at maturation. However, not all sensitivity analyses performed for the base model might be completely generalizable to this study because the base model did not include spatial structure.

The scarcity of empirical data on the potential long-term evolutionary effects of reserves underlines the vital role that carefully constructed and calibrated models ought to assume in addressing this question. We offer the analyses reported here as a step toward meeting this challenge. The various considerations above have hopefully made it clear that simple models featuring just a few variables and parameters are unlikely to do justice to the rich ecological settings that drive natural and anthropogenic evolutionary changes in nature. While we therefore believe that a model of the complexity studied here is indeed required for obtaining practically relevant results, this implies a trade-off with having to assess the adequacy of the adopted structural assumptions and parameter values. We therefore systematically explored the sensitivity of our model results to various assumptions and parameters, as summarized in Figs 2–6 and A1–C1.

Yet, there were several assumptions that, for the sake of brevity, we could not test here. For example, a simplifying assumption made in our model is that the four evolving traits are not subject to pleiotropy or constrained by linkages. This simplification was made because there is very little information available on wild stocks of Atlantic cod with which we could have parameterized such constraints or genetic covariances. Our model predicted that the PMRN midpoint (and specifically the PMRN intercept) underwent the largest evolutionary change among all four modeled life-history traits (see also Dunlop et al. 2009b), suggesting that the inclusion of genetic covariances may not have had a large effect on model predictions with regard to this central finding.

Other simplifying assumptions implied by our modeling closed populations, excluding multi-species interactions, variable environmental conditions, or other evolving traits. One benefit of reserves is that they protect multiple species. Fisheries-induced evolution could alter species interactions (Gårdmark et al. 2003) and by only modeling a single species, we could be missing other possible reserve effects (Mangel and Levin 2005; Baskett et al. 2006, 2007a) especially when size- or location-specific predation affects the evolution of the traits explored here. Also, the spatial structure of our model was kept simple and could therefore not account for edge effects that develop when fishing is concentrated along reserve boundaries, or for localized fishing effort concentrating on previously untargeted areas, two spatial factors that can alter a reserve's effectiveness (Kaiser 2003; Roberts et al. 2005; Kellner et al. 2007). Finally, many other traits in addition to the traits we model here could evolve in response to fishing (Heino and Godø 2002; Walsh et al. 2006) and could be impacted differentially by the creation of a reserve. For example, population-level migration patterns or individual-level mobility may evolve in response to fishing (Jørgensen et al. 2008a; Thériault et al. 2008) or reserve implementation (Heino and Hanski 2001; Baskett et al.2007b; Miethe et al. 2009), effects we have not modeled here.

Management implications

Several findings from this study have management implications. First, reserves may reduce the evolutionary effects of fishing even in a migratory species. This is important because many commercially and ecologically important species migrate between feeding and spawning grounds. While it has been suggested that reserves would not be effective when individuals from reserves can spawn together with those from harvested areas, our results show that protection on the feeding grounds effectively reduces evolution. Second, feeding-ground reserves are capable of reducing fisheries-induced evolution, whereas spawning-ground reserves can exacerbate the evolutionary response toward earlier maturation. A clear management recommendation therefore is that if the goal is to reduce fisheries-induced maturation evolution, the reserve should not be placed in the stock's spawning grounds. Third, even when taking into account evolution caused by fishing, the implementation of reserves probably reduces yield over decadal timescales. It might have been thought that by mitigating yield-reducing evolutionary effects, implementing a reserve could improve yield, or at least keep it constant; our results show that this is mostly not the case, as such an effect only occurs in a narrow range of settings and only when a long-term perspective is taken. Fourth, evolutionary changes that are already well underway are difficult to reverse through implementing a reserve. Given that even stopping harvest altogether results only in a relatively slow recovery (Law and Grey 1989; Dunlop et al. 2009b, Enberg et al. 2009), a more effective management strategy is to prevent evolutionary changes from occurring in the first place, rather than trying to stop or reverse them once underway. Fifth, our results show that it is advisable to manage populations as a whole and account for potential stock structure, because fishing in one area may cause evolution that can drastically alter yield in another area.

How do the predictions of our model relate to current management practices of Atlantic cod and similar species? Protection of spawning aggregations of Atlantic cod has been proposed as an essential measure for ensuring the sustainability of exploited stocks (Vitale et al. 2008). Indeed, several closed areas currently implemented tend to focus protection on spawning grounds (Murawski et al. 2000; Hu and Wroblewski 2009). Although protection of spawning individuals may be important for demographic reasons, our results show that protecting individuals on feeding grounds is just as, if not more, important for safeguarding a stock against fisheries-induced evolution. This has implications for stocks such as Northeast Arctic cod for which the introduction of industrial trawling has led to high rates of exploitation in the stock's feeding grounds (Law and Grey 1989; Heino et al. 2002b; Godø 2003). Our results suggest that protecting this stock's feeding grounds is highly advisable as a means of counteracting the observed fisheries-induced maturation evolution toward younger ages and smaller sizes.

As mentioned previously, marine reserves may have benefits that go beyond effects on single species. For example, reserves may provide protection of critical habitat that could sustain fish productivity. Our model, being a single-species model without habitat dynamics, obviously cannot account for these added reserve benefits. We therefore recommend that the approach to assessing the evolutionary impacts of fishing proposed here should be incorporated as one element of an ecosystem-based approach to fisheries management (Francis et al. 2007). Of the many model-based studies of marine reserves (for a review, see Gerber et al. 2003), only a few have considered evolution (e.g., Trexler and Travis 2000; Baskett et al. 2005; Miethe et al. 2009), so we really have only just begun to examine the full suite of potential benefits and consequences of mitigating fisheries-induced evolution through the creation of marine reserves.

Over mere decades, fishing can cause evolutionary changes in key life-history traits governing growth, maturation, and reproductive investment. Evolutionary changes induced by fishing can have far-reaching consequences, possibly altering yield, recovery potential, stock stability, profits from a fishery, species interactions, and migration patterns (Jørgensen et al. 2007). As these evolutionary effects may be slow or difficult to reverse (Conover et al. 2009; Dunlop et al. 2009b; Enberg et al. 2009; Stenseth and Dunlop 2009), the precautionary approach warrants that managers consider evolution when planning and implementing sustainable harvesting practices. In particular, the establishment of marine reserves may reduce the evolutionary effects of fishing, but appropriate reserve placement taking into account the spatial patterns of fisheries-induced selection pressures is crucial to their success.

Acknowledgements

Financial support for this project was provided to M.H. and E.D. by the Norwegian Research Council, to M.H. and U.D. by the European Research Network on Fisheries-induced Evolution, and to E.D., M.H., and U.D. by the European Union Training Network on Fisheries-induced Adaptive Change. We thank members of the FishACE network and of the University of Bergen's Evo-Fish and Modeling groups for helpful discussion of this work.

Literature cited

Almany, G. R., M. L. Berumen, S. R. Thorrold, S. Planes, and G. P. Jones. 2007. Local replenishment of coral reef fish populations in a marine reserve. Science 316:742-744.

Arlinghaus, R., S. Matsumura, and U. Dieckmann. 2009. Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). Evolutionary Applications 2:335-355.

Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Long-term trend in the maturation reaction norm of two cod stocks. Ecological Applications 14:1257-1271.

Baskett, M. L., S. A. Levin, S. D. Gaines, and J. Dushoff. 2005. Marine reserve design and the evolution of size at maturation in harvested fish. Ecological Applications 15:882-901.

Baskett, M. L., F. Micheli, and S. A. Levin. 2007. Designing marine reserves for interacting species: Insights from theory. Biological Conservation 137:163-179.

Baskett, M. L., M. Yoklavich, and M. S. Love. 2006. Predation, competition, and the recovery of overexploited fish stocks in marine reserves. Canadian Journal of Fisheries and Aquatic Sciences 63:1214-1229.

Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecology Letters 4:144-150.

Browman, H. I., C. T. Marshall, and R. Law. 2008. The role of fisheries-induced evolution. Science 320:47.

Comeau, L. A., S. E. Campana, and G. A. Chouinard. 2002. Timing of Atlantic cod (*Gadus morhua* L.) seasonal migrations in the southern Gulf of St Lawrence: interannual variability and proximate control. ICES Journal of Marine Science 59:333-351.

Conover, D. O., L. M. Clarke, S. B. Munch, and G. N. Wagner. 2006. Spatial and temporal scales of adaptive divergence in marine fishes and the implications for conservation. Journal of Fish Biology 69:21-47.

Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297:94-96.

Conover, D. O., and S. B. Munch. 2007. Faith, evolution, and the burden of proof. Fisheries 32:90-91.

Conover, D. O., S. B. Munch, and S. A. Arnott. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. Proceedings of the Royal Society B-Biological Sciences 276:2015-2020.

Costanza, R., F. Andrade, P. Antunes, M. van den Belt, D. Boersma, D. F. Boesch, F. Catarino et al. 1998. Principles for sustainable governance of the oceans. Science 281:198-199.

Dieckmann, U., and M. Heino. 2007. Probabilistic maturation reaction norms: Their history, strengths, and limitations. Marine Ecology Progress Series 335:253-269.

Dunlop, E.S., K. Enberg, C. Jørgensen, and M. Heino. 2009. Towards Darwinian fisheries management. Evolutionary Applications 2:245-259.

Dunlop, E. S., M. Heino, and U. Dieckmann. 2009. Eco-genetic modeling of contemporary life-history evolution. Ecological Applications 19:1815-1834.

Dunlop, E. S., B. J. Shuter, and U. Dieckmann. 2007. Demographic and evolutionary consequences of selective mortality: predictions from an eco-genetic model for smallmouth bass. Transactions of the American Fisheries Society 136:749-765.

Enberg, K., C. Jørgensen, E. S. Dunlop, M. Heino, and U. Dieckmann. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evolutionary Applications 2:394-414.

Ernande, B., U. Dieckmann, and M. Heino. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proceedings of the Royal Society of London Series B-Biological Sciences 271:415-423.

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to Quantitative Genetics. Essex, U.K., Longman.

Francis, R. C., M. A. Hixon, M. E. Clarke, S. A. Murawski, and S. Ralston. 2007. Fisheries management - Ten commandments for ecosystem-based fisheries scientists. Fisheries 32:217-233.

Gårdmark, A., U. Dieckmann, and P. Lundberg. 2003. Life-history evolution in harvested populations: the role of natural predation. Evolutionary Ecology Research 5:239-257.

Gårdmark, A., N. Jonzen, and M. Mangel. 2006. Density-dependent body growth reduces the potential of marine reserves to enhance yields. Journal of Applied Ecology 43:61-69.

Gaylord, B., S. D. Gaines, D. A. Siegel, and M. H. Carr. 2005. Marine reserves exploit population structure and life history in potentially improving fisheries yields. Ecological Applications 15:2180-2191.

Gell, F. R., and C. M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends in Ecology & Evolution 18:448-455.

Gerber, L. R., L. W. Botsford, A. Hastings, H. P. Possingham, S. D. Gaines, S. R. Palumbi, and S. Andelman. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications 13:S47-S64.

Gerber, L. R., S. S. Heppell, F. Ballantyne, and E. Sala. 2005. The role of dispersal and demography in determining the efficacy of marine reserves. Canadian Journal of Fisheries and Aquatic Sciences 62:863-871.

Godø, O. R. 2003. Fluctuation in stock properties of north-east Arctic cod related to long-term environmental changes. Fish and Fisheries 4:121-137.

Grift, R. E., A. D. Rijnsdorp, S. Barot, M. Heino, and U. Dieckmann. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Marine Ecology-Progress Series 257:247-257.

Grimm, V., and S. F. Railsback. 2005. Individual-based Modeling and Ecology: Princeton Series in Theoretical and Computational Biology. Princeton, NJ, USA, Princeton University Press.

Guenette, S., and T. J. Pitcher. 1999. An age-structured model showing the benefits of marine reserves in controlling overexploitation. Fisheries Research 39:295-303.

Halpern, B. S. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications 13:S117-S137.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters 5:361-366.

Hannesson, R. 1998. Marine reserves: what would they accomplish? Marine Resources Economics 13:159-170.

Hart, D. R. 2006. When do marine reserves increase fishery yield? Canadian Journal of Fisheries and Aquatic Sciences 63:1445-1449.

Hastings, A., and L. Botsford. 1999. Equivalence in yield from marine reserves and traditional fisheries management Science 284:1537-1538.

Heino, M. 1998. Management of evolving fish stocks. Canadian Journal of Fisheries and Aquatic Sciences 55:1971-1982.

Heino, M., L. Baulier, D. S. Boukal, E. S. Dunlop, S. Eliassen, K. Enberg, C. Jørgensen et al. 2008. Evolution of growth in Gulf of St Lawrence cod? Proceedings of the Royal Society B-Biological Sciences 275:1111-1112.

Heino, M., U. Dieckmann, and O. R. Godø. 2002a. Measuring probabilistic reaction norms for age and size at maturation. Evolution 56:669-678.

Heino, M., U. Dieckmann, and O. R. Godø. 2002b. Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod. ICES CM 2002/Y:14.

Heino, M., and O. R. Godø. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science 70:639-656.

Hilborn, R. 2006. Faith-based fisheries. Fisheries 31:554-555.

Hilborn, R., F. Micheli, and G. A. De Leo. 2006. Integrating marine protected areas with catch regulation. Canadian Journal of Fisheries and Aquatic Sciences 63:642-649.

Hilborn, R., K. Stokes, J. J. Maguire, T. Smith, L. W. Botsford, M. Mangel, J. Orensanz et al. 2004. When can marine reserves improve fisheries management? Ocean & Coastal Management 47:197-205.

Hilborn, R., and C. J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. New York, NY, U.S.A., Chapman & Hall.

Houle, D. 1992. Comparing evolvability and variability of quantitative traits. Genetics 130:195-204.

Hu, L. M., and J. S. Wroblewski. 2009. Conserving a subpopulation of the northern Atlantic cod metapopulation with a marine protected area. Aquatic Conservation-Marine and Freshwater Ecosystems 19:178-193.

Hunter, E., J. D. Metcalfe, and J. D. Reynolds. 2003. Migration route and spawning area fidelity by North Sea plaice. Proceedings of the Royal Society of London Series B-Biological Sciences 270:2097-2103.

Hutchings, J. A., and D. J. Fraser. 2008. The nature of fisheries- and farming-induced evolution. Molecular Ecology 17:294-313.

Hutchinson, W. F., G. R. Carvalho, and S. I. Rogers. 2001. Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. Marine Ecology-Progress Series 223:251-260.

ICES. 2007. Report of the Arctic Fisheries Working Group ICES C.M. 2007.

Jones, P. J. S. 2007. Point-of-View: Arguments for conventional fisheries management and against no-take marine protected areas: only half of the story? Reviews in Fish Biology and Fisheries 17:31-43.

Jonsdottir, O. D. B., A. K. Imsland, A. K. Danielsdottir, V. Thorsteinsson, and G. Naevdal. 1999. Genetic differentiation among Atlantic cod in south and south-east Icelandic waters: synaptophysin (Syp I) and haemoglobin (HbI) variation. Journal of Fish Biology 54:1259-1274.

Jørgensen, C., E. S. Dunlop, A. F. Opdal, and Ø. Fiksen. 2008a. The evolution of spawning migrations: state dependence and fishing-induced changes. Ecology 89:3436-3448.

Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Ernande et al. 2008b. The role of fisheries-induced evolution - Response. Science 320:48-50.

Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Ernande et al. 2007. Managing evolving fish stocks. Science 318:1247-1248.

Jørgensen, C., B. Ernande, and Ø. Fiksen. 2009. Size-selective fishing gear and life history evolution in the Northeast Arctic cod. Evolutionary Applications 2:356–370.

Kaiser, M. J. 2003. Are closed areas the solution? Marine Conservation 5:11.

Kaiser, M. J. 2005. Are marine protected areas a red herring or fisheries panacea? Canadian Journal of Fisheries and Aquatic Sciences 62:1194-1199.

Kellner, J. B., I. Tetreault, S. D. Gaines, and R. M. Nisbet. 2007. Fishing the line near marine reserves in single and multispecies fisheries. Ecological Applications 17:1039-1054.

Kennedy, J., P. R. Witthames, and R. D. M. Nash. 2007. The concept of fecundity regulation in plaice (*Pleuronectes platessa*) tested on three Irish Sea spawning populations. Canadian Journal of Fisheries and Aquatic Sciences 64:587-601.

Kirkpatrick, M. 1993. The evolution of size and growth in harvested natural populations, Pages 145-154 *in* T. K. Stokes, J. M. McGlade, and R. Law, eds. The Exploitation of Evolving Resources. Berlin, Germany, Springer-Verlag.

Kjesbu, O. S., P. R. Witthames, P. Solemdal, and M. G. Walker. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. Journal of Sea Research 40:303-321.

Kramer, D. L., and M. R. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. Environmental Biology of Fishes 55:65-79.

Kuparinen, A., and J. Merilä. 2007. Detecting and managing fisheries-induced evolution. Trends in Ecology & Evolution 22:652-659.

Kuparinen, A., and J. Merilä. 2008. The role of fisheries-induced evolution. Science 320:47-48.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57:659-668.

Law, R. 2007. Fisheries-induced evolution: present status and future directions. Marine Ecology-Progress Series 335:271-277.

Law, R., and D. R. Grey. 1989. Evolution of yields from populations with age-specific cropping. Evolutionary Ecology 3:343-359.

Lester, N. P., B. J. Shuter, and P. A. Abrams. 2004. Interpreting the von Bertalanffy model of somatic growth in fish: the cost of reproduction. Proceedings of the Royal Society of London Series B-Biological Sciences 271:1625-1631.

Lloret, J., and H. J. Ratz. 2000. Condition of cod (*Gadus morhua*) off Greenland during 1982-1998. Fisheries Research 48:79-86.

Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: The emerging science of marine reserves. Ecological Applications 13:S3-S7.

Mangel, M., and P. S. Levin. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. Philosophical Transactions of the Royal Society B-Biological Sciences 360:95-105.

Marshall, C. T., C. L. Needle, N. A. Yaragina, A. M. Ajiad, and E. Gusev. 2004. Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. Canadian Journal of Fisheries and Aquatic Sciences 61:1900-1917.

Marshall, C. T., N. A. Yaragina, B. Ådlandsvik, and A. V. Dolgov. 2000. Reconstructing the stock-recruit relationship for Northeast Arctic cod using a bioenergetic index of reproductive potential. Canadian Journal of Fisheries and Aquatic Sciences 57:2433-2442.

McEvoy, L. A., and J. McEvoy. 1992. Multiple spawning in several commercial fish species and its consequences for fisheries management, cultivation and experimentation. Journal of Fish Biology 41:125-136.

McIntyre, T. M., and J. A. Hutchings. 2003. Small-scale temporal and spatial variation in Atlantic cod (*Gadus morhua*) life history. Canadian Journal of Fisheries and Aquatic Sciences 60:1111-1121.

Miethe, T., J. Pitchford, and C. Dytham. 2009. An Individual-based model for reviewing marine reserves in the light of fisheries-induced evolution in mobility and size at maturation. Journal of the Northwest Atlantic Fisheries Society 41:151-162.

Mollet, F. M., S. B. M. Kraak, and A. D. Rijnsdorp. 2007. Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. Marine Ecology-Progress Series 351:189-199.

Mousseau, T. A., and D. A. Roff. 1987. Natural selection and the heritability of fitness components. Heredity 59:181-198.

Murawski, S. A., R. Brown, H. L. Lai, P. J. Rago, and L. Hendrickson. 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank experience. Bulletin of Mathematical Biology 66:775-798.

Okamoto, K., R. Whitlock, P. Magnan, and U. Dieckmann. 2009. Mitigating fisheries-induced evolution in lacustrine brook trout (*Salvelinus fontinalis*) in southern Quebec, Canada. Evolutionary Applications 2:415-437.

Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428:932-935.

Olsen, E. M., G. R. Lilly, M. Heino, J. Morgan, J. Brattey, and U. Dieckmann. 2005. Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 62:811-823.

Oskarsson, G. J., O. S. Kjesbu, and A. Slotte. 2002. Predictions of realised fecundity and spawning time in Norwegian spring-spawning herring (*Clupea harengus*). Journal of Sea Research 48:59-79.

Palsson, O. K., and V. Thorsteinsson. 2003. Migration patterns, ambient temperature, and growth of Icelandic cod (*Gadus morhua*): evidence from storage tag data. Canadian Journal of Fisheries and Aquatic Sciences 60:1409-1423.

Pampoulie, C., D. E. Ruzzante, V. Chosson, T. D. Jorundsdottir, L. Taylor, V. Thorsteinsson, A. K. Danielsdottir et al. 2006. The genetic structure of Atlantic cod (*Gadus morhua*) around Iceland: insight from microsatellites, the Pan I locus, and tagging experiments. Canadian Journal of Fisheries and Aquatic Sciences 63:2660-2674.

Pauly, D., V. Christensen, S. Guenette, T. J. Pitcher, U. R. Sumaila, C. J. Walters, R. Watson et al. 2002. Towards sustainability in world fisheries. Nature 418:689-695.

Perez-Ruzafa, A., M. Gonzalez-Wanguemert, P. Lenfant, C. Marcos, and J. A. Garcia-Charton. 2006. Effects of fishing protection on the genetic structure of fish populations. Biological Conservation 129:244-255.

Ricker, W. E. 1981. Changes in average size and average age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 38:1636-1656.

Roberts, C. M., J. A. Bohnsack, F. Gell, J. P. Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. Science 294:1920-1923.

Roberts, C. M., J. P. Hawkins, and F. R. Gell. 2005. The role of marine reserves in achieving sustainable fisheries. Philosophical Transactions of the Royal Society B-Biological Sciences 360:123-132.

Robichaud, D., and G. A. Rose. 2000. Multiyear homing of Atlantic cod. Canadian Journal of Fisheries and Aquatic Sciences 58:2325-2329.

Robichaud, D., and G. A. Rose. 2001. Multiyear homing of Atlantic cod to a spawning ground. Canadian Journal of Fisheries and Aquatic Sciences 58:2325-2329.

Robichaud, D., and G. A. Rose. 2004. Migratory behaviour and range in Atlantic cod: inference from a century of tagging. Fish and Fisheries 5:185-214.

Rose, G. A. 1993. Cod spawning on a migration highway in the North-West Atlantic. Nature 366:458-461.

Rose, G. A., and R. L. O'Driscoll. 2002. Capelin are good for cod: can the northern stock rebuild without them? ICES Journal of Marine Science 59:1018-1026.

Roughgarden, J. 1979, Theory of population genetics and evolutionary ecology: An introduction. New York, NY, U.S.A., Macmillan publishing Co., Inc.

Stearns, S. C. 1992, The evolution of life histories. Oxford, U.K., Oxford University Press.

Stenseth, N. C., and E. S. Dunlop. 2009. Unnatural selection. Nature 457:803-804.

Svedäng, H., D. Righton, and P. Jonsson. 2007. Defining 'natal homing' in marine fish populations; need for inference in fishery science: reply to Bradbury & Laurel (2007). Marine Ecology-Progress Series 349:309-310.

Swain, D. P., A. F. Sinclair, and J. M. Hanson. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proceedings of the Royal Society B-Biological Sciences 274:1015–1022.

Swain, D. P., A. F. Sinclair, and J. M. Hanson. 2008. Evolution of growth in Gulf of St Lawrence cod: reply to Heino et al. Proceedings of the Royal Society of London B-Biological Sciences 275:1113-1115.

Thériault, V., E. S. Dunlop, U. Dieckmann, L. Bernatchez, and J. J. Dodson. 2008. The impact of fishing-induced mortality on the evolution of alternative life-history tactics in brook charr. Evolutionary Applications 1:409-423.

Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal homing in a marine fish metapopulation. Science 291:297-299.

Thorsen, A., and O. S. Kjesbu. 2001. A rapid method for estimation of oocyte size and potential fecundity in Atlantic cod using a computer-aided particle analysis system. Journal of Sea Research 46:295-308.

Trexler, J. C., and J. Travis. 2000. Can marine protected areas restore and conserve stock attributes of reef fishes? Bulletin of Marine Science 66:853-873.

Vitale, F., P. Borjesson, H. Svedang, and A. Casini. 2008. The spatial distribution of cod (*Gadus morhua* L.) spawning grounds in the Kattegat, eastern North Sea. Fisheries Research 90:36-44.

Walsh, M. R., S. B. Munch, S. Chiba, and D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecology Letters 9:142-148.

Wang, H.-Y., and T. O. Höök. 2009. Eco-genetic model to explore fishing-induced ecological and evolutionary effects on growth and maturation schedules. Evolutionary Applications 2:438–455.

Table 1. Parameter values for the eco-genetic model of Atlantic cod.

Description	Symbol	Equation	Value	Source
Initial mean genetic PMRN intercept (cm)	$\bar{i}_{\mathrm{G},0}$	–	93 (90.3)	1
Initial mean genetic PMRN slope (cm yr^{-1})	$\bar{s}_{\mathrm{G},0}$	–	–0.052 (–0.052)	1
Initial mean genetic gonado-somatic index	$\bar{r}_{\mathrm{G},0}$	–	0.12 (0.12)	1
Initial mean genetic growth capacity (cm)	$\bar{g}_{\mathrm{G},0}$	–	12.8 (12.9)	1
Initial genetic coefficient of variation	$C_{\mathrm{G},0}$	–	0.08	2
Initial heritability	$h^2_{x,0}$	–	0.2	2
Default retention probability	q	1a-d	0.8	3
PMRN width (cm)	w	2c	25.9	4
Density-dependent growth constant (g^{-1})	b	3a	$1.02\cdot10^{-8}$	5
Density-dependent growth exponent	c	3a	0.3	5
Weight-specific oocyte density (g^{-1})	d	–	$4.4\cdot10^{3}$	6
Conversion factor for gonado-somatic index	δ	3c	1.73	7
Proportionality constant for weight (g $\mathrm{cm}^{-\beta}$)	α	4a	$3.2\cdot10^{-3}$	8
Exponent of length-weight allometry	β	4a	3.24	8
Density-independent stock-recruitment constant	k	4b	$5.3\cdot10^{-3}$	9
Density-dependent stock-recruitment constant	j	4b	$8.3\cdot10^{5}$	10
Maximal growth increment (cm)	$g_{\max}$	5a	80	11
Background natural mortality probability	p_{B}	–	0.02	12
Minimum-size limit on feeding grounds (cm)	l_{F}	–	60	13

Values in parentheses are mean pre-fishing equilibrium trait values, averaged over 30 independent model runs. PMRN = probabilistic maturation reaction norm.

Rationale and sources: (1) Set so that the pre-fishing equilibrium of evolving traits is reached within 2000 yrs and values are within empirical ranges for Atlantic cod reported for PMRNs (Heino et al. 2002b; Olsen et al. 2004), gonado-somatic indeces (Lloret and Ratz 2000; Rose and O'Driscoll 2002; McIntyre and Hutchings 2003), and growth rates (Marshall et al. 2004; Olsen et al. 2005; ICES 2007). (2) Within the range reported by Houle (1992) and Mousseau and Roff (1987). (3) Model assumption. (4) Olsen et al. (2005). (5) Set so that the range of phenotypic growth rates predicted by the model is within the empirical range for Atlantic cod (Marshall et al. 2004; Olsen et al. 2005; ICES 2007). (6) Thorsen and Kjesbu (2001). (7) Lester et al. (2004). (8) From survey data for 1999-2007 collected by the Norwegian Institute of Marine Research (O.R. Kjesbu, pers. comm.). (9) Marshall et al. (2000). (10) Scaled from Marshall et al. (2000) so that population abundance at pre-fishing equilibrium is computationally manageable (ca. 20,000). (11) Set so that growth capacity at pre-fishing equilibrium produces phenotypic growth rates within the empirical range for Atlantic cod (Marshall et al. 2004; Olsen et al. 2005; ICES 2007). (12) Set so that the total natural mortality probability equals 0.18 (ICES 2007). (13) Model assumption as in Dunlop et al. (2009b).

Figure captions

Figure 1. Schematic illustration of the eco-genetic model of Atlantic cod. Processes that occur in each area, either in the feeding grounds or in the spawning grounds, are indicated within the boxes. The initial spawning location in the spawning grounds and the initial landing location of the larvae in the feeding grounds are chosen in proportion to the area of the locations.

Figure 2. Effects of a spawning-ground reserve (left) and feeding-ground reserve (right) on fisheries-induced evolution of maturation, growth and reproductive investment. The feeding-ground proportion of catch (R_F) represents the fraction of the total allowable catch that is permitted in the feeding grounds relative to the spawning grounds. Line and symbol thickness increases with increasing R_F between 0 (all fishing is in the spawning grounds) and 1 (all fishing is in the feeding grounds). Fishing occurred for 100 years with an annual harvest ratio of 0.5. The length at 50% maturation probability is the midpoint of the probabilistic maturation reaction norm (PMRN) for the mean age at maturation (8 years) in the initial population, $l_{\mathrm{p50,8}} = 8s_\mathrm{G} + i_\mathrm{G}$, where s_G is the genetic PMRN slope and i_G is the genetic PMRN intercept. Genetic growth capacity (g_G) describes the maximum potential average growth effort without density dependence. The genetic gonado-somatic index (r_G) is the genetic measure of reproductive investment. The horizontal dashed line indicates the value of the trait in the year before fishing is started when the population was at an evolutionary and ecological equilibrium. Values shown are means for 30 independent model runs. Legend in panel B applies to all panels.

Figure 3. Effects of a spawning-ground reserve (left) and feeding-ground reserve (right) on catch from the fishery. The feeding-ground ratio (R_F) of catches represents the fraction of the total allowable catch that is permitted in the feeding grounds relative to the spawning grounds.

The thickness of lines and symbols increases with increasing R_F between 0 (all fishing is in the spawning grounds) and 1 (all fishing is in the feeding grounds). Fishing occurred for 100 years with an annual harvest ratio of 0.5. Values shown are means for 30 independent model runs. Legend in panel B applies to all panels.

Figure 4. Effects of movement between the reserve and harvested area influencing the effectiveness of a feeding-ground reserve. The continuous line corresponds to the default retention probability of 0.8, while the dashed line refers to a retention probability of 0.2. All fishing was in the feeding grounds ($R_F = 1$) and occurred for 100 years with an annual harvest ratio of 0.5. Values shown are means for 30 independent model runs. Legend in panel B applies to all panels.

Figure 5. Effects of fishing for 50 years followed by the creation of a feeding-ground reserve. All fishing takes place in the feeding grounds ($R_F = 1$). Three different annual harvest ratios (0.2, 0.4, and 0.6) and reserve areas (0.2, 0.4, and 0.6) are considered Fishing at these harvest ratios continued after the reserve was created. Reserve area increases with line thickness. Values shown are means for 30 independent model runs. Legend in panel B applies to all panels.

Figure 6. Effects of fishing for 50 years followed by the creation of a feeding-ground reserve. The annual harvest ratio was 0.6 in the stock's feeding grounds ($R_F = 1$) and was continued before and after creation of the reserve. Three different reserve areas are considered (0.2, 0.4, and 0.6); reserve area increases with line thickness. The dashed lines describe a population that is not protected by a reserve. Values shown are means for 30 independent model runs. Legend in panel B applies to both panels.

Figure 1.

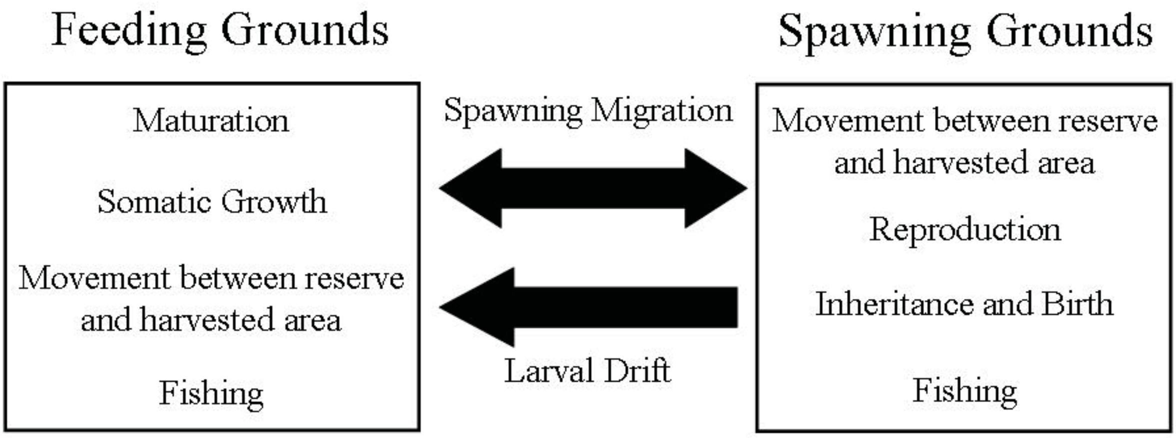

Feeding Grounds
Spawning Grounds
Maturation
Somatic Growth
Movement between reserve and harvested area
Fishing
Spawning Migration
Larval Drift
Movement between reserve and harvested area
Reproduction
Inheritance and Birth
Fishing

Figure 2.

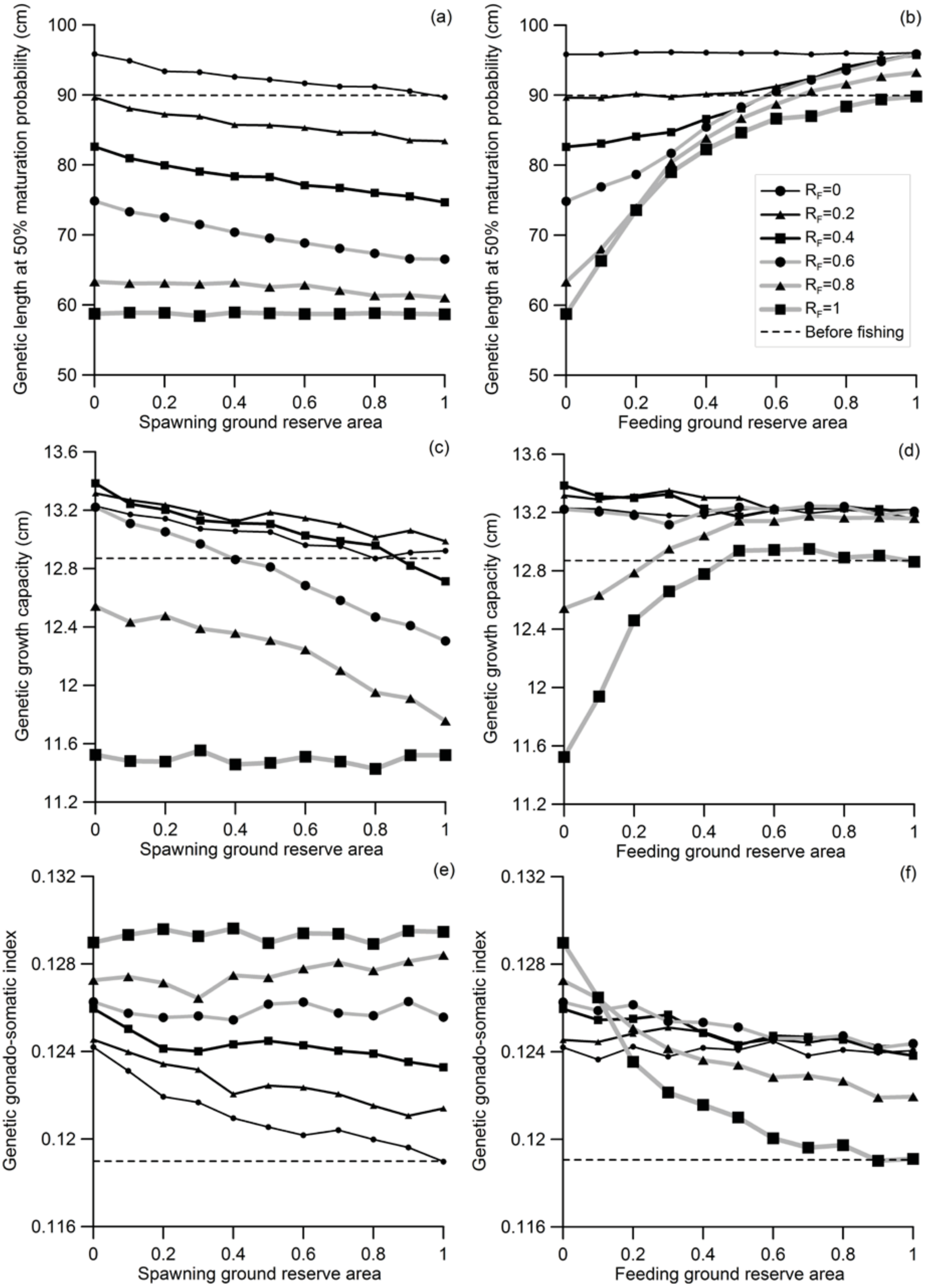
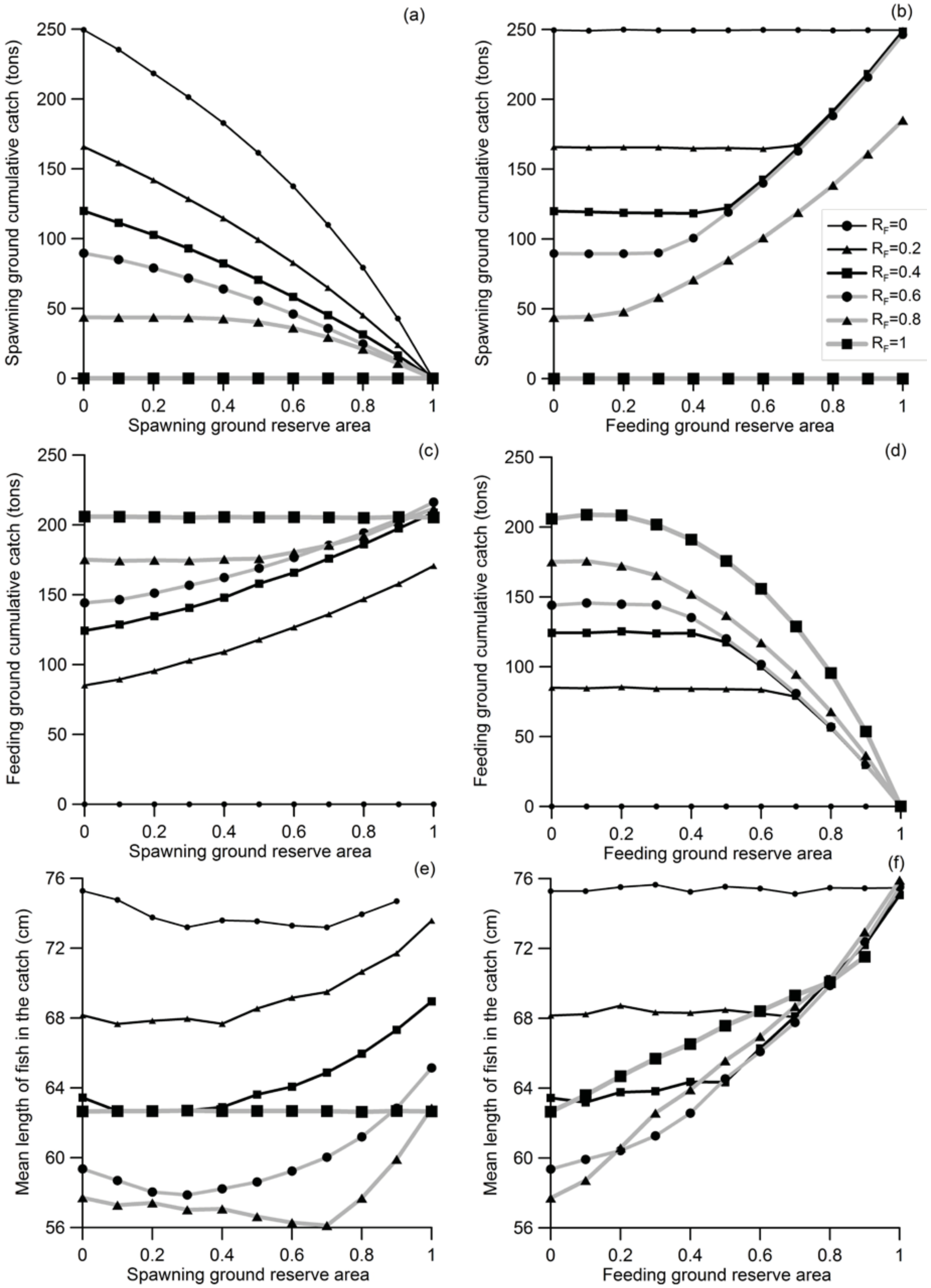
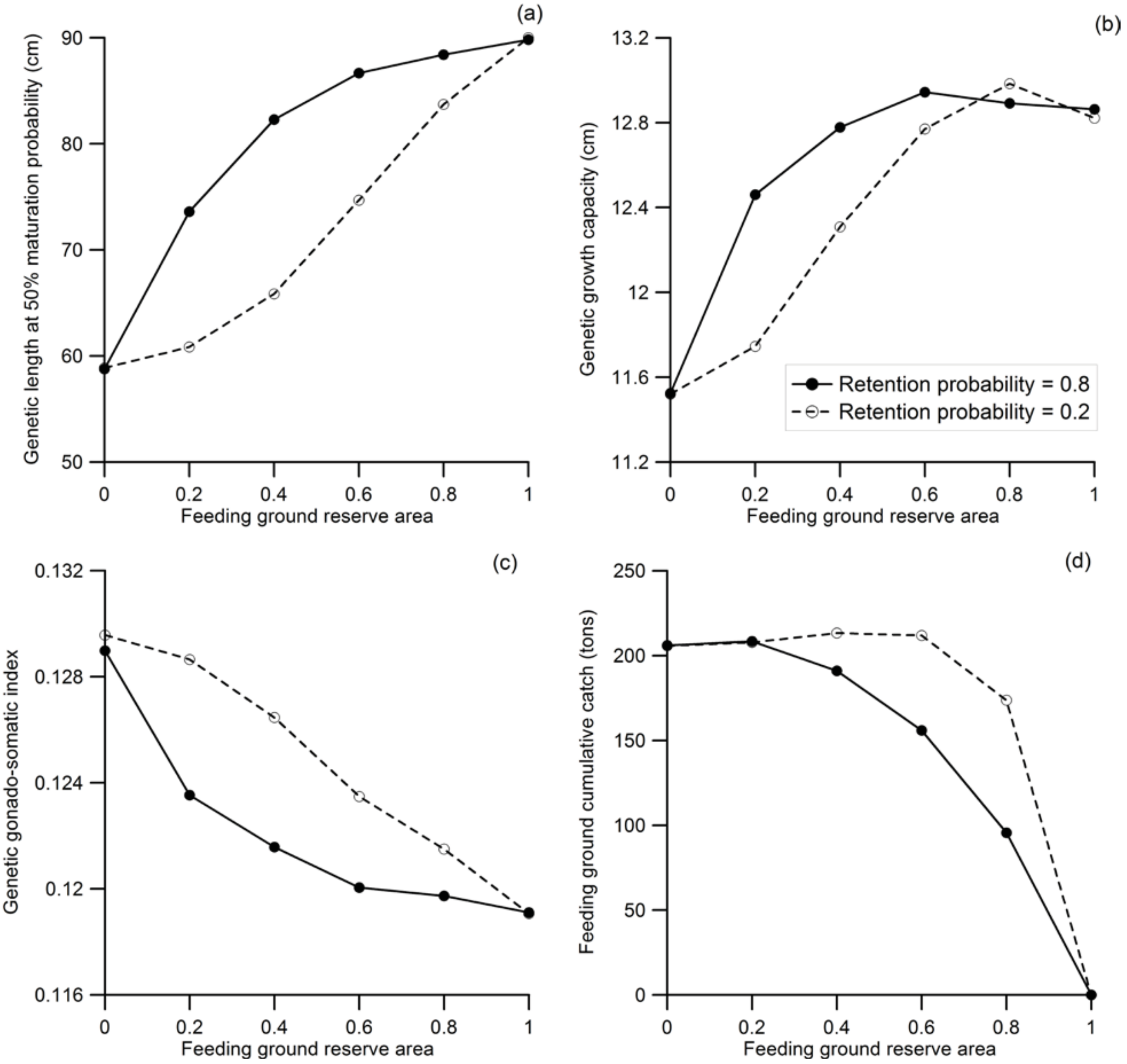

(a)
(b)
Genetic length at 50% maturation probability (cm)
100
90
80
70
60
50
0
0.2
0.4
0.6
0.8
1
Spawning ground reserve area
Feeding ground reserve area
R_F=0
R_F=0.2
R_F=0.4
R_F=0.6
R_F=0.8
R_F=1
Before fishing
(c)
(d)
Genetic growth capacity (cm)
13.6
13.2
12.8
12.4
12
11.6
11.2
(e)
(f)
Genetic gonado-somatic index
0.132
0.128
0.124
0.12
0.116

Figure 3.

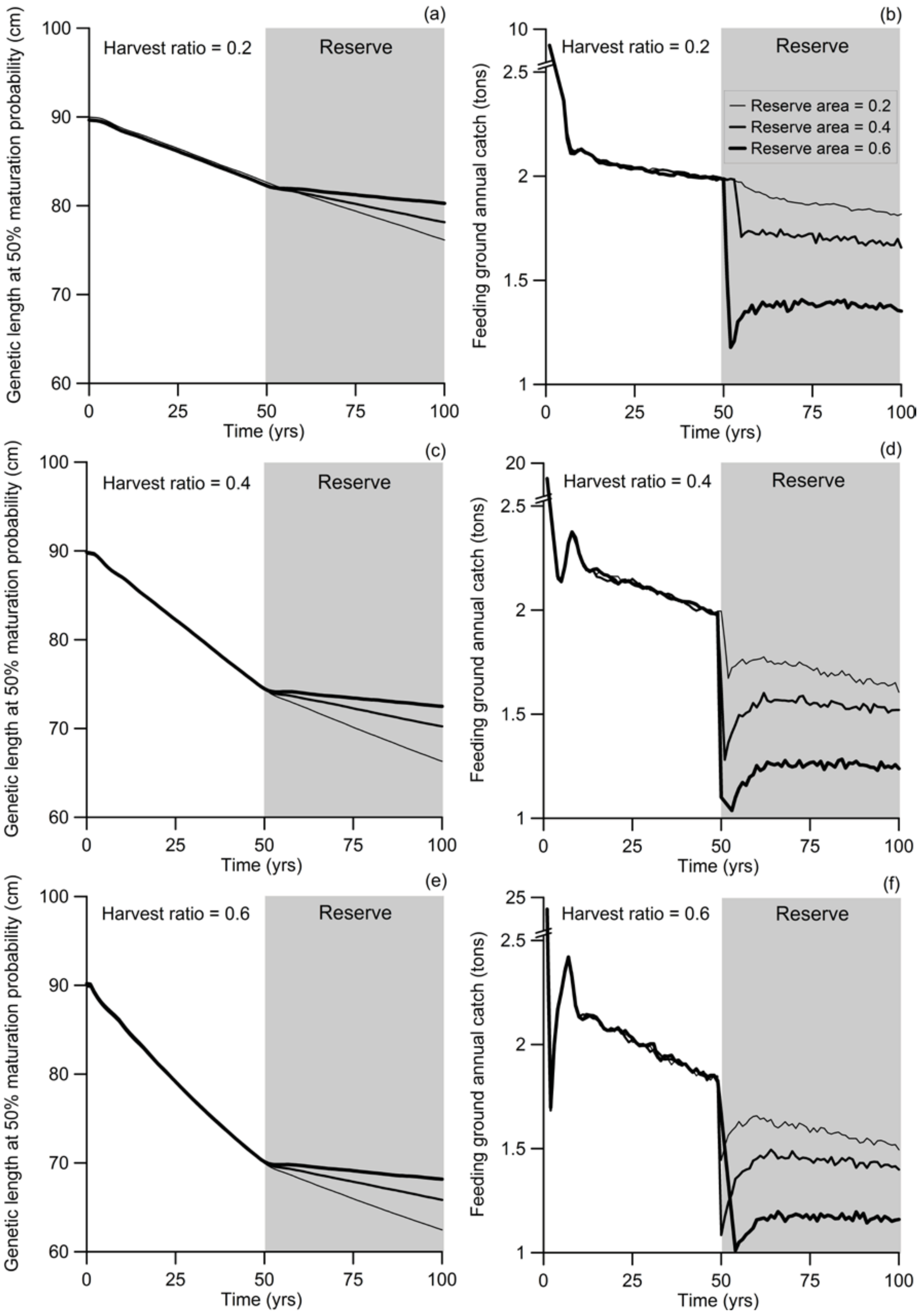

(a)
Spawning ground cumulative catch (tons)
250
200
150
100
50
0
0
0.2
0.4
0.6
0.8
1
Spawning ground reserve area
(b)
Spawning ground cumulative catch (tons)
Feeding ground reserve area
R_F=0
R_F=0.2
R_F=0.4
R_F=0.6
R_F=0.8
R_F=1
(c)
Feeding ground cumulative catch (tons)
Spawning ground reserve area
(d)
Feeding ground cumulative catch (tons)
Feeding ground reserve area
(e)
Mean length of fish in the catch (cm)
76
72
68
64
60
56
Spawning ground reserve area
(f)
Mean length of fish in the catch (cm)
Feeding ground reserve area

1058 Figure 4.



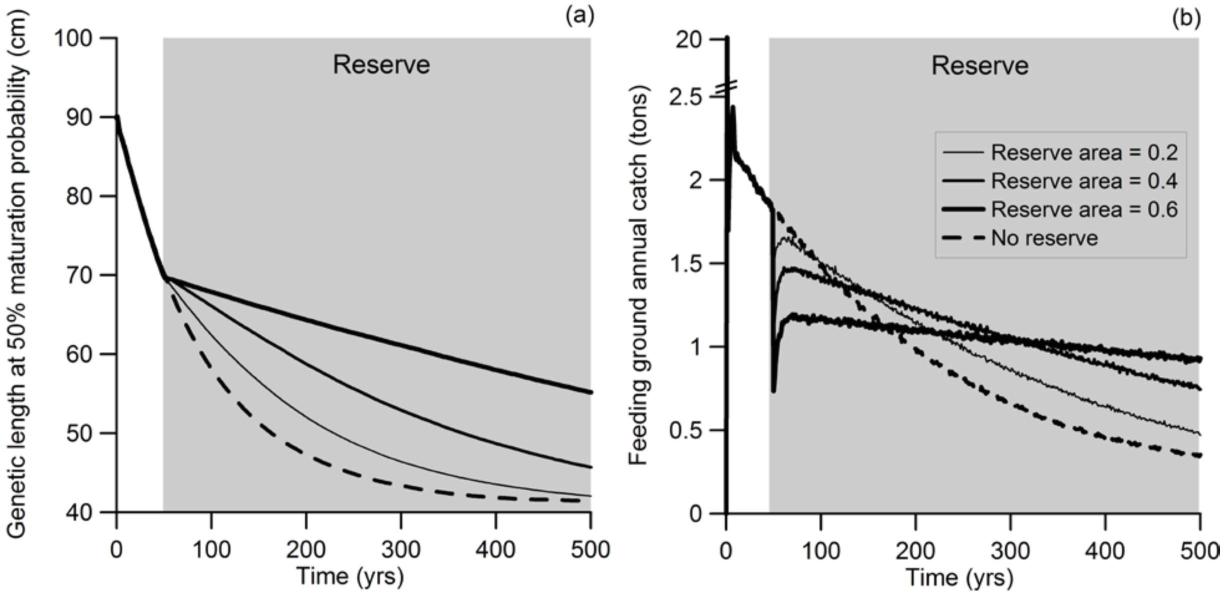
1059

1060 Figure 5.



1061

1062 Figure 6.



1063

Appendix A. Effect of natal homing on spawning-ground and feeding-ground reserves

In this appendix, we examine the influence of incorporating natal homing in our model. When natal homing is introduced, individuals in the population have a tendency to spawn in their area of birth. In other words, an individual born in a spawning-ground reserve will tend to return to that spawning-ground reserve for spawning. Individuals have only a ‘tendency’ to return, because there is movement between the harvested area and the reserve that introduces some variability in whether an individual actually returns to their area of birth (eqns 1a-d in the main text).

Results of this investigation show very little difference between situations with and without natal homing (there is little difference between the left and right columns in Fig. A1); this was true for both a spawning-ground reserve and for a feeding-ground reserve. Changing the retention probability q did influence predictions, but natal homing had little effect on those predictions. For a feeding ground reserve, there was more evolution to smaller lengths at 50% genetic maturation probability (owing mainly to a decrease in the probabilistic maturation reaction norm intercept), higher GSIs, and smaller genetic growth capacities (Fig. A1) when the retention rate parameter was low (i.e., when there was more movement between the reserve and harvested area). For a spawning ground reserve, the difference between results for the two retention probabilities was less than for a feeding-ground reserve. For a spawning-ground reserve, lower retention probabilities (and therefore more movement) led to evolution of larger lengths at 50% genetic maturation probability, higher genetic growth capacity, and higher genetic GSI (Fig. A1). Therefore, with the exception of the GSI, more movement coupled with a spawning-ground reserve had an opposite effect of more movement coupled with a feeding ground reserve. This is perhaps not surprising given the different selective pressures acting when fishing occurs in the spawning grounds s opposed to in the feeding grounds (as discussed in more detail in the main text).

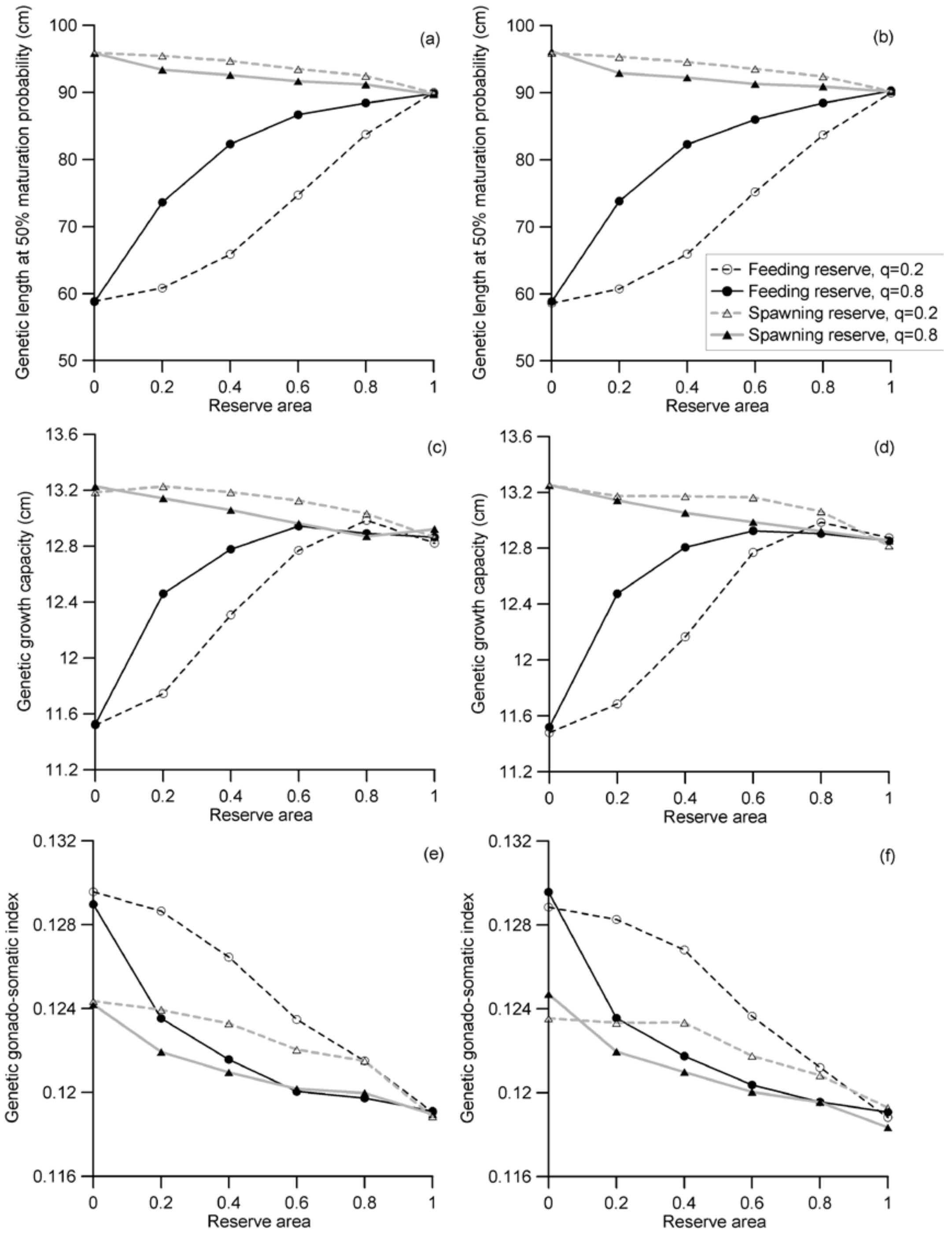


Figure A1 Influence of natal homing on the effectiveness of a reserve. Fishing occurs in the spawning grounds when the reserve is located in the spawning grounds, and fishing occurs in the feeding grounds when the reserve is located in the feeding grounds. Fishing occurs for 100 years with an annual harvest ratio of 0.5. Panels on the left (A, C, E) are for a population without natal homing (default) and panels on the right (B, D, F) are for populations in which there is a tendency for individuals to spawn in the area of their birth. The retention probability *q* was also varied (eqns 1a–d in the main text). Values shown are means for 30 independent model runs. Legend in panel B applies to all panels.

Appendix B. Effect of a reserve on a population without annual spawning migration

In this appendix, we test the impact of a reserve on fisheries-induced evolution in a species that does not undergo an annual spawning migration. The harvestable biomass for this type of reserve is equal to the biomass of individuals above the minimum-size limit in the reserve and the harvested area. Everything else is equivalent to the baseline model described in the main text.

Results of this investigation show that the difference between a population that annually migrates to spawning grounds and a population that does not migrate depends on the area of the reserve and on the annual harvest ratio (Fig. B1). For low annual harvest ratios and small to medium reserve areas, a reserve created for a nonmigrating population results in less evolution than a feeding-ground reserve created for a migrating population (Fig. B1). This is a likely result of the genetic mixing that occurs in the spawning grounds during reproduction when there is an annual spawning migration. An individual occupying the feeding-ground reserve could mate with an individual that occupies the feeding ground's harvested area, resulting in offspring trait values that will average between the two parental trait values.

Generally, a feeding-ground reserve has an effect more similar to a reserve created for a nonmigrating population than to a spawning-ground reserve created for a migrating population (Fig. B1). The reason for the higher similarity is that harvest pressure on juveniles and adults causes selection for earlier maturation; this selection pressure can be reduced by protecting the juveniles and adults that reside in the reserve. The dissimilarity between situations with a spawning-ground reserve and with a nonmigrating population occurs because there is no targeted fishery of spawning individuals in the later case. A fishery of spawning individuals creates selection pressures mostly in the opposite direction than a fishery for juveniles and adults, and the subsequent protection of spawning individuals through the creation of a spawning-ground reserve has very different implications than protecting juveniles and adults above a minimum-size limit.

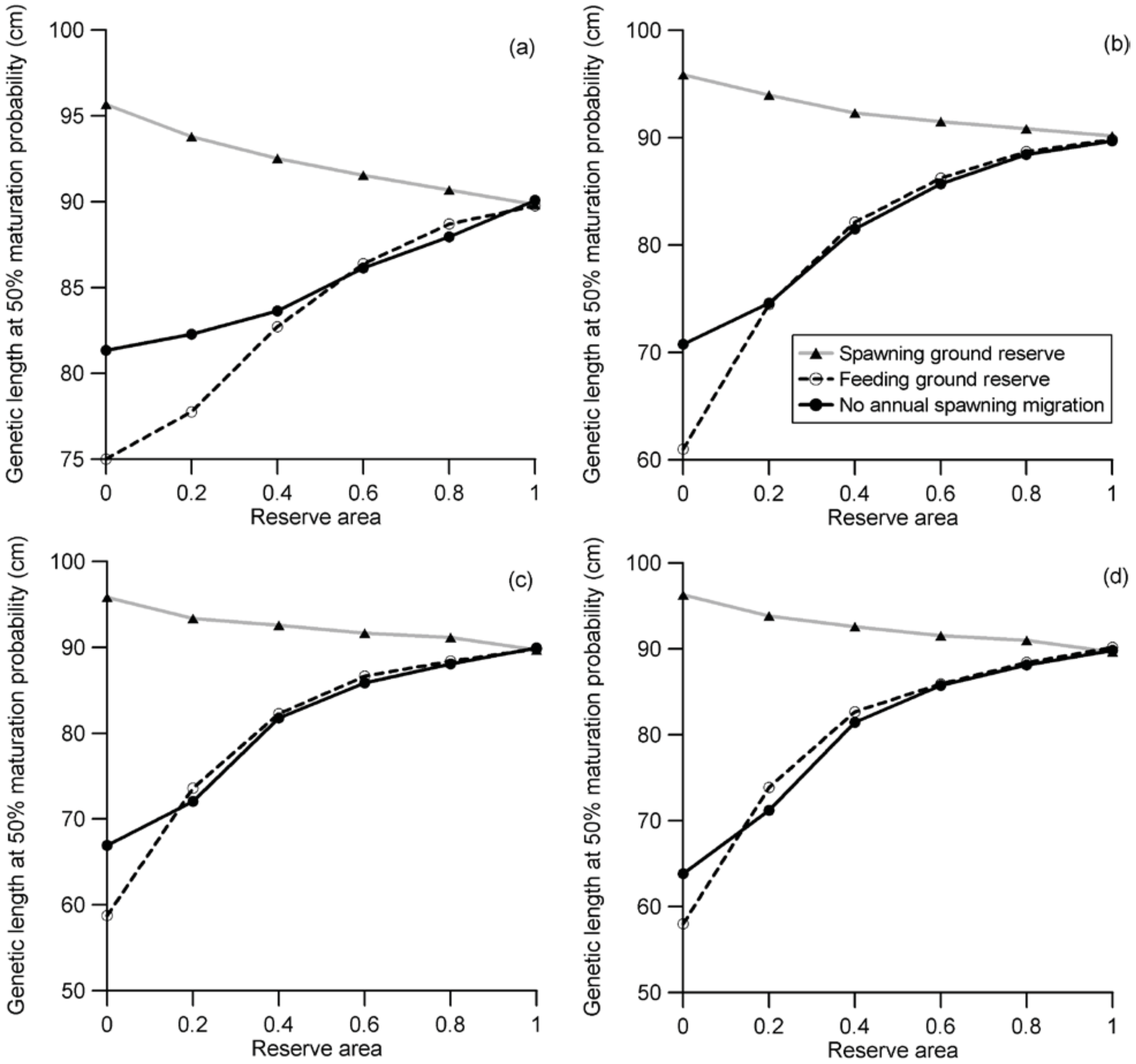


Figure B1 Influence of an annual spawning migration on the effectiveness of a reserve. Fishing occurs in the spawning grounds when the reserve is located in the spawning grounds, and fishing occurs in the feeding grounds when the reserve is located in the feeding grounds. Fishing occurs for 100 years with an annual harvest ratio of 0.2 (a), 0.4 (b), 0.5 (c), or 0.6 (d). Values shown are means for 30 independent model runs. Legend in panel B applies to all panels.

Appendix C. Effect of excluding effort displacement

In the model presented in the main text, harvestable biomass is determined as the biomass of all harvestable individuals in the reserve and the harvested area. This was to account for the effort displacement that can occur when a reserve is created. In this appendix, we test a scenario, in which the harvestable biomass equals the harvestable biomass in the harvested area, so that the former is unaffected by biomass in the reserve and no effort displacement occurs.

We examine this scenario by considering fishing that occurs for 50 years prior to the creation of a feeding-ground reserve. Our results show that effort displacement generally causes little difference in the effect of a reserve on evolution (Fig. C1). The only difference occurs for low annual harvest ratios and small reserve areas (Fig. C1). In cases showing a difference, the reserve is less effective at curbing evolution when there is effort displacement (Fig. C1).

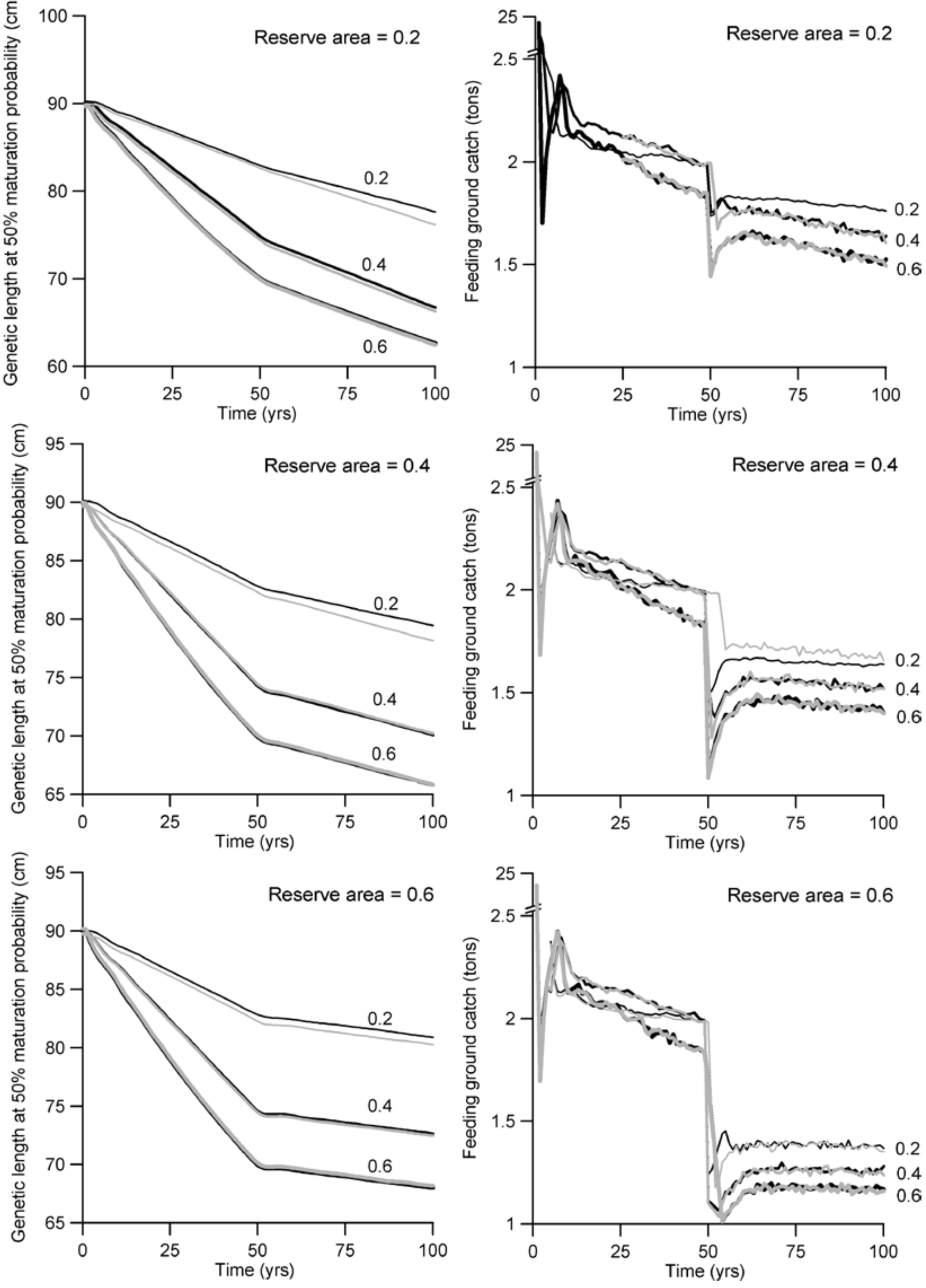


Figure C1 Effect of changing the measure of harvestable biomass. Grey lines describe settings with effort displacement, in which the harvestable biomass equaled the harvestable biomass in the reserve and the harvested area (default). Black lines describe settings without effort displacement, in which the harvestable biomass equaled the harvestable biomass in the harvested area alone. Line thickness increases with the annual harvest ratio (0.2, 0.4, and 0.6). Fishing occurs for 50 years followed by the creation of a feeding-ground reserve. Values shown are means for 30 independent model runs.