Effects of fishing on growth traits: a simulation analysis

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Abstract—Fisheries often target individuals based on size. Size-selective fishing can create selection differentials on life-history traits and, when those traits have a genetic basis, may cause evolution. The evolution of life-history traits affects potential yield and sustainability of fishing, and it is therefore an issue for fishery management. Yet fishery managers usually disregard the possibility of evolution, because little guidance is available to predict evolutionary consequences of management strategies. We attempt to provide some generic guidance. We develop an individual-based model of a population with overlapping generations and continuous reproduction. We simulate model populations under size-selective fishing to generate and quantify selection differentials on growth. The analysis comprises a variety of common life-history and fishery characteristics: variability in growth, correlation between von Bertalanffy growth parameters (K and L_∞), maturity rate, natural mortality rate (M), M/K ratio, duration of spawning season, fishing mortality rate (F), maximum size limit, slope of selectivity curve, age at 50% selectivity, and duration of fishing season. We found that each characteristic affected the magnitude of selection differentials. The most vulnerable stocks were those with a short spawning or fishing season. Under almost all life-history and fishery characteristics examined, selection differentials created by realistic fishing mortality rates are considerable.

Fishing is typically size selective. It almost always targets the larger individuals of a population and can thus shift the spawning stock towards smaller, slower-growing individuals. If somatic growth has some genetic basis, size-selective fishing may cause evolution toward a smaller size-at-age.

Changes in somatic growth are well documented in field data, and several studies implicate fishing (Ricker, 1981; Harris and McGovern, 1997; Haugen and Vøllestad, 2001; Sinclair et al., 2002). However, with typical field data, it is difficult to rule out other explanations. Changes in growth could result from fluctuations in population density or the environment. Furthermore, they may not be evolutionary, but instead expressions of phenotypic variability. Because of such possibilities, the idea that fishing can cause evolution has often been accepted because of compelling theoretical arguments, rather than on empirical support. However, the laboratory experiments of Conover and Munch (2002) demonstrated that size selection can cause evolution of growth traits. More and more, fishing-induced evolution is considered not just possible, but prevalent (Law, 2000; Stockwell et al., 2003).

The evolution of growth traits, despite wide acknowledgement of the potential for evolution of these traits, is usually a low priority in fishery management. However, it raises at least four management concerns. First, any reduction in growth rate or maximum size can decrease recreational and economic value (Miller and Kapuscinski, 1994). Second, size selection could reduce genetic variability (Falconer and Mackay, 1996),

unpredictably altering correlated traits and population fitness. Third, evolution may not easily be reversed, even with after-the-fact management. Fourth, the evolution of growth and other life-history traits can modify population dynamics (Bronikowski et al., 2002; Shertzer and Ellner, 2002) and therefore potential yield (Edley and Law, 1988; Heino 1998). Evolution in fishes can be rapid (Reznick et al., 1997; Hendry et al., 2000; Quinn et al., 2001), so that evolutionary, population, and fishery dynamics occur on similar time-scales (Sinervo et al., 2000; Shertzer et al., 2002; Yoshida et al., 2003). These dynamics imply that evolution matters for fishery management on the time-scale of years or decades.

For fishing to cause evolution, two conditions must be met. There must be a selection differential on a phenotypic trait and a genetic basis must exist for the trait's expression (i.e., the trait must be heritable). Selection differential is defined as the difference in the mean phenotypic trait value of parents before and after selection (e.g., size-selective fishing). Stokes and Law (2000) argued that, under exploitation levels in many of today's fisheries, "selection differentials on body size should be substantial and measurable." Even so, attempts to estimate selection differentials of actual fish stocks have been rare (but see Law and Rowell, 1993; Miller and Kapuscinski, 1994). This lack of estimates is surprising, given that the data needed are often available, as noted by Law (2001).

The second necessary condition, heritability, is defined as the proportion of phenotypic variability in offspring

that is due to the genotypes of the parents. It can range from zero to one, with a higher value potentially speeding the evolutionary response to selection. Field estimates of heritability in fish size are uncommon because in nature it is difficult (although not impossible; McAllister et al., 1992) to separate genetic and environmental effects on phenotypes. Almost all estimates come from laboratory experiments (e.g., Hadley et al., 1991; Conover and Munch, 2002; Vandeputte et al., 2002), mostly on populations from aquaculture breeding programs (e.g., Gjedrem, 1983; Jarayabhand and Thavornyutikarn, 1995; Henryon et al., 2002). One might expect laboratory experiments to over-estimate natural heritabilities, because experiments tend to reduce environmental effects on total phenotypic variance, but estimates from the laboratory have been similar to those from the field (Weigensberg and Roff, 1996). The laboratory experiments indicate that heritabilities in fish growth traits may vary widely among populations but are high enough to allow rapid evolution, given a large enough selection differential.
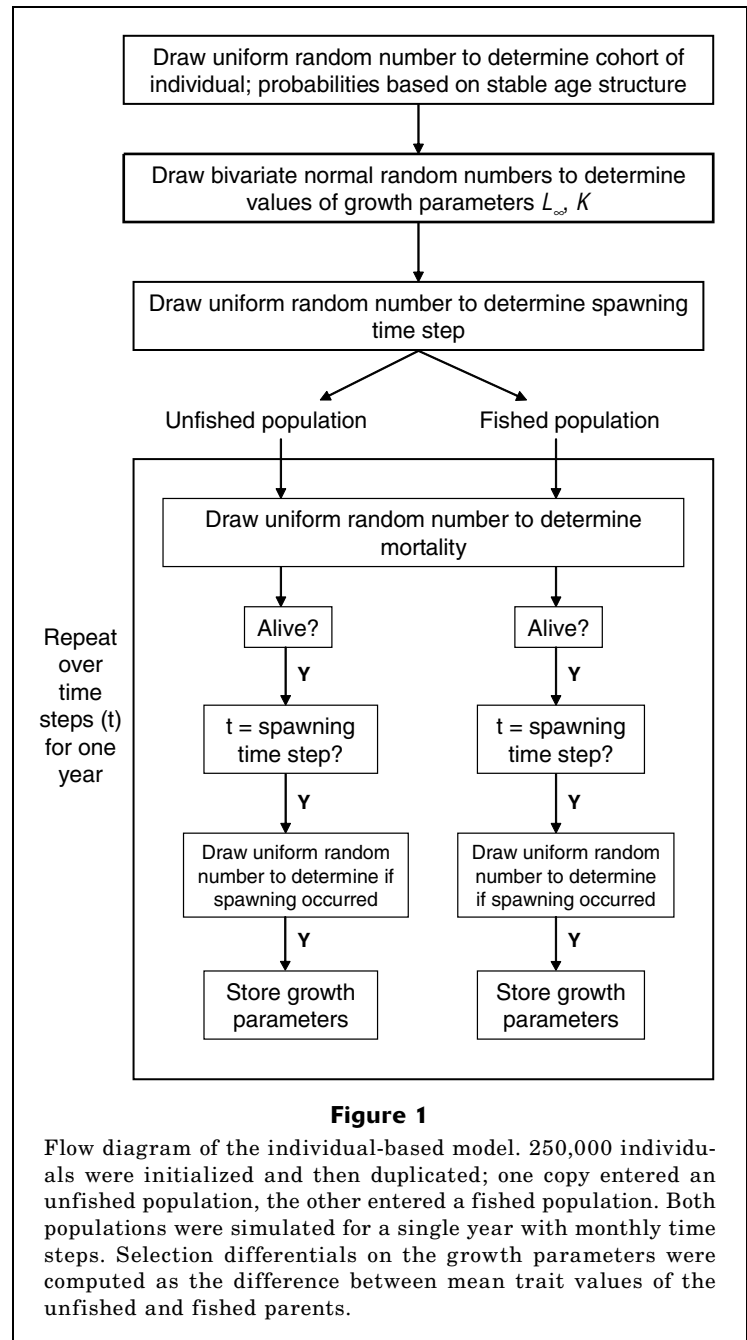
Models of evolutionary response to selective harvest have usually taken one of two approaches: quantitative genetics (e.g., Law, 1991; Ratner and Lande, 2001) or life-history optimization (e.g., Blythe and Stokes, 1999). In the present study, we take a different approach. Rather than attempt to predict evolution explicitly, we focus on selection differentials, a necessary (but not sufficient) condition for an evolutionary response.

We use simulation analyses to compute selection differentials caused by fishing. The simulation model is one common in fisheries. It consists of an age-structured population following von Bertalanffy growth, with fishing and reproduction modeled as continuous processes.

Our goal is to compare selection differentials across a variety of life-history and fishery characteristics. We quantify selection differentials on growth parameters and body size. If growth traits are heritable, those life-history and fishery characteristics with the largest selection differentials are most likely to generate an evolutionary response. Armed with such knowledge, fishery managers can weigh potential evolutionary effects when choosing a fishing strategy.

Materials and methods

To compute selection differentials caused by size-selective fishing we used an individual-based model (Fig. 1). To initialize the model, 250,000 individual phenotypes were generated. Each was assigned a set of life-history parameters and then duplicated. One copy entered an unfished population that experienced only natural mortality; the

Figure 1

Flow diagram of the individual-based model. 250,000 individuals were initialized and then duplicated; one copy entered an unfished population, the other entered a fished population. Both populations were simulated for a single year with monthly time steps. Selection differentials on the growth parameters were computed as the difference between mean trait values of the unfished and fished parents.

other copy entered a fished population that experienced both natural and fishing mortality. Growth, survival, and reproductive success of individuals were simulated with monthly time steps for a single year. At the end of the simulation, selection differentials on growth parameters were computed as the percent change between the mean values of spawners in the two populations.

Model structure

The model comprised three basic life-history functions: growth, survival, and reproduction. For each individual,

size was assumed a function of age (a) and followed the von Bertalanffy model,

$$l(a) = L_\infty[1 - e^{-K(a-t_0)}], \tag{1}$$

where $l(a)$ = the length-at-age of an individual;
L_∞ = the theoretical maximum length;
K = the growth rate, and
t_0 = the theoretical age when size would have been zero.

In our study, each individual's age and size were updated at each monthly time step.

Survival was computed differently for the two populations. In the unfished population, individuals survived with a probability depending only on the natural mortality rate (M/yr). In the fished population, individuals survived with a probability depending on both the natural mortality rate and the size-specific fishing mortality rate. Size selectivity [$s(l)$] by the fishery increased with length according to the logistic equation

$$s(l) = \frac{1}{1 + e^{-\beta_s(l-L_s)}}, \tag{2}$$

where β_s = the slope of the selectivity curve; and
L_s = the length at 50% selectivity.

The function $s(l)$ describes the proportion of the fully-selected fishing mortality rate (F) experienced by individuals of length l. The size-specific fishing mortality rate, therefore, is $s(l)F$ per year. Fishing was applied over a fishing season of duration D_F.

The probability of reproduction was assumed equal to the probability of maturity [$m(a)$]. In the model, maturity increases with age and is independent of length. Although maturity likely relates to length through bioenergetics, the relationship was not modeled here because it is, in general, poorly understood. Like selectivity (Eq. 2), $m(a)$ was modeled by a logistic equation, but with a slope parameter, β_m, and age at 50% maturity, A_m.

In nature, values of life-history parameters K and A_m are related to a stock's natural mortality rate. A higher natural mortality rate reduces the expected lifespan and consequently tends to be associated with a higher growth rate (K) and a younger age at maturity (A_m). In the simulation, K and A_m were related to natural mortality by life-history invariants (detailed later). Life-history invariants have a strong theoretical and empirical basis (Roff, 1984; Beverton, 1992; Charnov, 1993) and have been valuable in other fishery applications (Mangel, 1996; Charnov and Skuladottir, 2000; Frisk et al., 2001; Williams and Shertzer, 2003).

Simulation

To initialize the simulation, individuals were assigned at random to a cohort. The number of cohorts was determined as the age at which approximately 1% of the population would be expected to remain under natural mortality [$-\ln(0.01)/M$, rounded to the nearest integer]. Probabilities of cohort membership decayed exponentially with age according to M; the probability of the oldest cohort was adjusted to include the remaining fraction of fish (i.e., a plus group). The probabilities were scaled to sum to one, and a uniform random number was drawn to determine an individual's cohort.

Next, individuals were assigned parameter values for von Bertalanffy growth. The value of t_0 was fixed at 0.5 yr. Values of L_∞ and K were chosen uniquely for each individual. Following Xiao (1994), L_∞ and K were assumed to follow a bivariate normal distribution with standard deviations σ_L and σ_K, respectively, and correlation ρ.

Finally, individuals were assigned a time step (month) within the year to attempt spawning. The time step was chosen from months distributed uniformly over a spawning season of duration, D_s.

Once assigned parameter values, each individual was duplicated. One copy entered the unfished population, the other the fished population. The populations were simulated in parallel over a single model year.

The simulation iterated each individual through monthly time steps. At each step, the simulation computed growth and checked for survival and reproduction. In the unfished population, the monthly probability of survival was $\exp(-M/12)$. In the fished population, the monthly probability of survival during the fishing season depended on natural mortality and on the size-specific fishing mortality. For simplicity, we assumed size within a month was fixed so that that the probability of survival was $\exp[(-M/12-s(l_0)F)/D_F]$, where l_0 was an individual's size at the beginning of the month. Outside the fishing season, only natural mortality applied. To check for survival, a uniform random number was drawn and compared to the survival probability appropriate for the population.

Each individual surviving to its assigned spawning time had the opportunity to reproduce. In that case, a uniform random number was drawn and compared to the probability of reproduction. If reproduction was successful, the individual's growth parameters went into a pool of parents used to compute selection differentials.

Growth parameters L_∞ and K jointly determine size-at-age, and it is on these parameters that we describe selection differentials. At the end of the simulation year, we computed a selection differential on each growth parameter as the percent difference between mean trait values (L_∞ or K) of the unfished and fished parents. Based on the differences in L_∞ and K, we also computed upper and lower bounds of selection differentials on size-at-age. The bounds occur where age approaches t_0 or ∞. Because each population consisted of the same set of individuals at the beginning of the year, any difference in growth traits between parents at the end of the year could be attributed solely to fishing.

Base model and variations

We began with a base model built on parameter values chosen or computed to represent common life-history and

Table 1

Parameter values used in the base model. Formulas for the growth rate (K) and the age at 50% maturity (A_m) are life-history invariant relationships from Charnov (1993) and Beverton (1992), respectively. The formula for L_s is the length at age A_m according to von Bertalanffy growth. A value of ∞ for slope parameters corresponds to a knife-edge curve.

Parameter	Description	Formula	Value
M	Natural mortality rate (per year)	Fixed	0.2
F	Fishing mortality rate (per year)	Fixed	0 to 10
$\bar{L}_\infty$	Mean asymptotic size in growth function	Fixed	1000
$\bar{K}$	Mean growth rate in growth function	$M/1.65$	0.12
t_0	Location parameter in growth function	Fixed	−0.5
CV_L	Coefficient of variation in L_∞	Fixed	20%
CV_K	Coefficient of variation in K	Fixed	20%
ρ	Correlation between L_∞ and K	Fixed	0
β_s	Slope of the size selectivity curve	Fixed	∞
β_m	Slope of the maturity curve	Fixed	∞
A_m	Age at 50% maturity	$\log\left[(3\bar{K}+M)/M\right]/\bar{K}$	8.55
L_s	Length at 50% selectivity	$\bar{L}_\infty\left[1-\exp\left(-\bar{K}[A_m-t_0]\right)\right]$	666
D_S	Duration of spawning season (yr)	Fixed	1
D_F	Duration of fishing season (yr)	Fixed	1

fishery characteristics (Table 1). We then conducted a variety of sensitivity analyses.

In the base model, the natural mortality rate (M) was set at 0.2/yr, a value common for many fish species. Sensitivity analyses used M = 0.1, 0.4, or 0.8. The value of M affects the values of K, A_m, and L_s, according to the life-history invariant relationships (Table 1). The relationship between M and K is often referred to as the M/K ratio. Charnov (1993) suggested a central value for fishes of M/K=1.65, which we used in the base model. Beverton (1992) examined the M/K ratio for fishes and found a range of 0.5 to 2.5. We used this range in our sensitivity analyses to examine the effect of the M/K ratio on selection differentials (Table 2).

The base model treated L_∞ and K as independent variables (ρ=0, Table 1). Often these parameters are correlated. A meta-analysis by He and Stewart (2001) of 235 fish populations indicated a correlation value of −0.28. The negative correlation could be expected from a trade-off between growth rate (represented by K) and maximum size (represented by L_∞), as has been suggested in studies of bioenergetics (Stearns, 1992; Hutchings, 1993; Mangel, 1996). Our sensitivity analyses considered negative values of correlation that range from −0.25 to −1.

With the base model, selectivity and maturity were assumed to be "knife-edge," a functional form often used in fisheries for convenience. Also, in the base model the size at 50% selectivity (L_s) was assumed to occur at an age equal to the age at 50% maturity (A_m). Although

these fishery characteristics are common, selectivity and maturity may not be knife-edge or coincide. In sensitivity analyses, we examined different shapes of selectivity and maturity curves (Fig. 2). We also examined the affect of shifting the age at 50% selectivity from −2 to 2, in relation to the base case. This shift corresponds to a range in L_s values from 574 to 738. For simplicity, we held F constant for these sensitivity analyses, implying constant effort but resulting in different amounts of removals.

Under logistic selectivity, the oldest, largest fish receive the highest rate of exploitation. Yet often the largest fish are unavailable to a fishery because of migration patterns or regulations (e.g., a maximum size limit). Thus our sensitivity analyses included a cap on susceptible sizes. The cap was set at 70, 80, or 90% of L_∞.

Using the base model, we examined the effects of annual fishing mortality rate over values that range from F=0 to F=10/yr, which is 0 to 50 times the natural mortality rate. Fishing mortality was applied continuously throughout the year (i.e., D_F=1). In sensitivity analyses, we examined shorter fishing seasons ranging from one to six months. The F was still an annual rate but was applied over fewer months and adjusted so that the number of fish removed was the same as when D_F=1. For seasons shorter than a full year, fishing was assumed to occur at the beginning of the year.

Like the fishing season, the duration of the spawning season was a full year in the base model (D_S=1).

Table 2

Percent selection differential on the von Bertalanffy growth coefficient (K) at fishing mortality = 0.8/yr. Columns correspond to the levels of the coefficient of variation (CV=0%, 10%, 20%) in K and in the asymptotic length (L_∞). Any combination with 0% CV in K is not presented because it results in zero selection differential. The first row corresponds to the base model and subsequent rows correspond to changes in the base model: correlation between L_∞ and K (ρ), slope of maturity curve (β_m), natural mortality (M), M/K ratio, duration of annual spawning season (D_S), maximum size limit (L_u), slope of selectivity curve (β_s), change in age at 50% selectivity (A_s) in relation to the base case, and duration of annual fishing season (D_F).
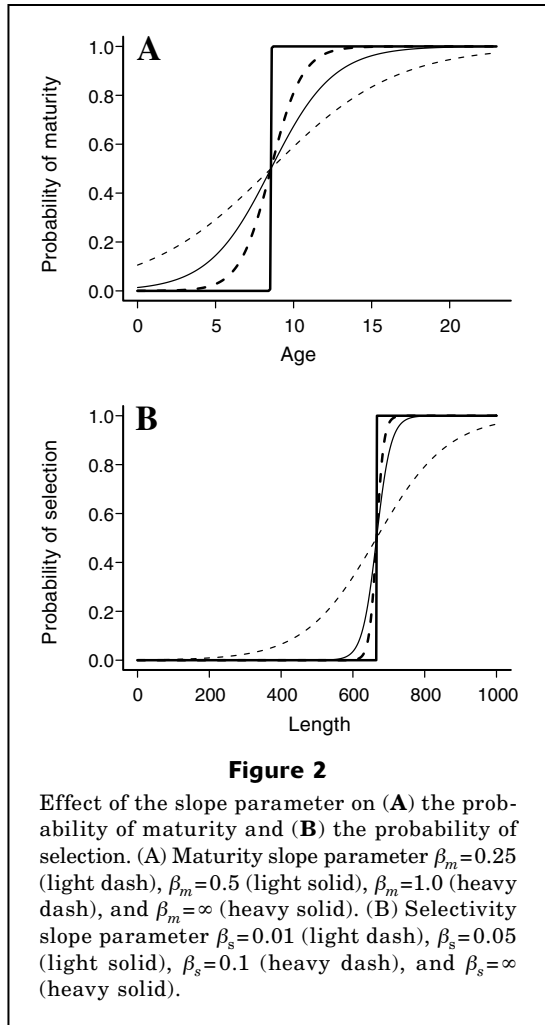
| | Parameter values | | | | | |
	L_∞: 0%CV K: 10%CV	L_∞: 10%CV K: 10%CV	L_∞: 20%CV K: 10%CV	L_∞: 0%CV K: 20%CV	L_∞:10%CV K: 20%CV	L_∞: 20%CV K: 20%CV
Base	0.7	0.5	0.3	2.1	1.7	1.2
$\rho = -1$	0.7	−0.7	−1.3	2.1	0.2	−2.3
$\rho = -0.75$	0.7	−0.3	−0.8	2.1	0.8	−0.9
$\rho = -0.5$	0.7	0.0	−0.4	2.1	1.1	0.1
$\rho = -0.25$	0.7	0.3	0.0	2.1	1.4	0.6
$\beta_m = 0.25$	0.2	0.2	0.1	0.7	0.7	0.6
$\beta_m = 0.5$	0.3	0.3	0.2	1.1	1.1	0.9
$\beta_m = 1$	0.5	0.4	0.3	1.7	1.4	1.1
$M = 0.1$	0.4	0.4	0.3	1.6	1.5	1.2
$M = 0.4$	0.7	0.4	0.3	2.0	1.5	1.0
$M = 0.8$	0.6	0.3	0.2	1.6	1.1	0.7
$M/K = 0.5$	0.6	0.3	0.1	1.9	1.0	0.6
$M/K = 1$	0.4	0.3	0.2	1.5	1.3	0.8
$M/K = 2$	0.5	0.4	0.3	1.9	1.6	1.2
$M/K = 2.5$	0.8	0.6	0.4	2.4	2.1	1.5
$D_S = 1/12$	1.6	1.0	0.6	4.5	3.6	2.3
$D_S = 3/12$	1.4	0.9	0.5	4.1	3.3	2.2
$D_S = 6/12$	1.1	0.8	0.5	3.3	2.7	1.8
$L_u = 700$	0.0	0.0	0.0	−0.1	−0.1	0.0
$L_u = 800$	0.2	0.0	0.0	0.3	0.2	0.0
$L_u = 900$	0.4	0.2	0.1	1.1	0.8	0.3
$\beta_s = 0.01$	0.3	0.2	0.2	1.1	1.0	0.8
$\beta_s = 0.05$	0.6	0.4	0.3	1.9	1.6	1.2
$\beta_s = 0.1$	0.6	0.5	0.3	2.0	1.7	1.2
$A_s = -2$	0.1	0.2	0.2	1.1	1.2	1.0
$A_s = -1$	0.4	0.4	0.3	1.7	1.6	1.1
$A_s = 1$	0.6	0.5	0.3	2.1	1.7	1.2
$A_s = 2$	0.5	0.4	0.3	1.9	1.6	1.1
$D_F = 1/12$	1.5	1.0	0.6	4.3	3.5	2.3
$D_F = 3/12$	1.3	0.9	0.6	3.9	3.1	2.1
$D_F = 6/12$	1.2	0.7	0.5	3.3	2.6	1.8

In sensitivity analyses, the spawning season ranged from one to six months and was assumed to occur at the end of the year.

A selection differential cannot exist without phenotypic variation. The base model assumed a coefficient of variation (CV) of 20% in both L_∞ and K. For sensitivity analyses, combinations of 0%, 10%, and 20% CV in L_∞ and K were examined for the influence of growth variability on selection differentials of L_∞ and K.
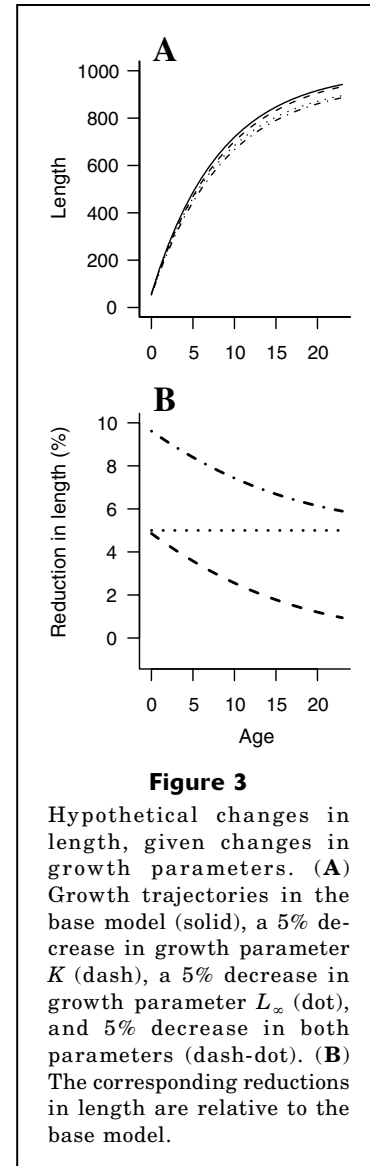
Results

Changes in growth parameters L_∞ and K affect size-at-age jointly, resulting in non-uniform selection differentials across ages (Fig. 3). The selection differentials on size are bounded by the differentials at the extreme ages, t_0 and ∞. At the youngest age, the selection differential on size is limited by the sum of the selection differentials on L_∞ and K plus their product. (At age t_0, the selection differential on size is undefined.) As age

Figure 2

Effect of the slope parameter on (**A**) the probability of maturity and (**B**) the probability of selection. (A) Maturity slope parameter β_m=0.25 (light dash), β_m=0.5 (light solid), β_m=1.0 (heavy dash), and β_m=∞ (heavy solid). (B) Selectivity slope parameter β_s=0.01 (light dash), β_s=0.05 (light solid), β_s=0.1 (heavy dash), and β_s=∞ (heavy solid).

Figure 3

Hypothetical changes in length, given changes in growth parameters. (**A**) Growth trajectories in the base model (solid), a 5% decrease in growth parameter K (dash), a 5% decrease in growth parameter L_∞ (dot), and 5% decrease in both parameters (dash-dot). (**B**) The corresponding reductions in length are relative to the base model.

increases, the selection differential on size increases or decreases monotonically toward an asymptote, the selection differential on L_∞. Thus selection differentials on size across all ages are bounded by those at $L_\infty + K + L_\infty K$ and L_∞. The selection differential on the smallest fish (age approaching t_0) is an upper bound when the selection differential on K is positive, and a lower bound when negative. These properties are important for interpreting how selection differentials on size-at-age correspond to differentials on L_∞ and K.

Using the base model, we computed selection differentials on L_∞ and K as functions of fishing mortality, over the range F=0 to F=10/yr. The selection differentials increased with F nonlinearly, resulting in a concave relationship (Fig. 4). However for F<2.0, the relationship is nearly linear.

The alternative models also revealed linear relationships between selection differentials and F, for F<2.0 (figures not shown). In addition, those relationships have a zero intercept (by definition, no fishing, no selection differential). Because the relationships are (nearly) linear and have a common intercept, the rank of selec-

tion differentials among models does not change across values of F. A model that bears the highest selection differential at F=0.2 does so at F=2.0. We therefore present results of sensitivity analyses for a single value of F (F=0.8/yr), with the understanding that for other values of F (up to 2.0), magnitudes of selection differentials can be inferred and ranks among models are maintained.

Increased variation in L_∞ and K tended to increase the selection differentials, and interaction between the two growth parameters (Tables 2 and 3). Selection differentials on L_∞ were generally larger than those on K. In the base model, the largest selection differential on each growth parameter occurred when variation in the focal parameter was highest and variation in the other parameter was zero. The selection differentials on size-at-age were largest when variation in both parameters was highest (20% CV for both L_∞ and K).

Life-history parameters

The correlation (ρ) between L_∞ and K was assumed to be zero in the base model and negative in sensitivity analyses. The effect of correlation depended on variation in the growth parameters. When the CV was zero for either parameter, correlation had no effect on selection differentials (Tables 2 and 3). When the CV was positive for both, a negative correlation decreased selection differentials in relation to those from the base model (Tables 2 and 3). For decreased values of the correlation coefficient (i.e., stronger negative correlation), the percent selection differentials on K decreased, whereas the percent selection differentials on L_∞ either decreased or remained constant. The percent selection differentials on the size near age t_0 ranged from 3.7% to –0.1% for values of ρ from 0 to –1. The percent selection differentials on L_∞ remained relatively constant, ranging from 2.1% to 2.5%, with the highest at $\rho=0$ (Fig. 5).

Knife-edge maturity ($\beta_m=\infty$) resulted in larger selection differentials than did other maturity curves (Tables 2 and 3). As the slope of the maturity curve became more gradual, the selection differentials decreased. For β_m values greater than 1, the selection differentials on size were similar to those of the knife-edge case (Fig. 5).
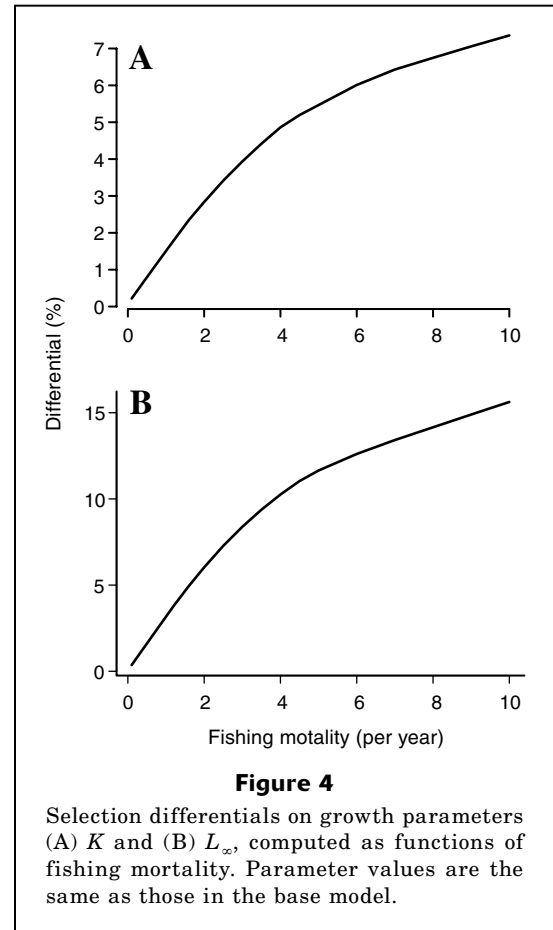
The effect of M on selection differentials was relatively small (Tables 2 and 3). Changes in M from 0.1 to 0.8 led to small changes in selection differentials (Fig. 5). The largest selection differentials tended to occur near intermediate values of M (Tables 2 and 3, Fig. 5). This nonlinear response in the selection differentials is not surprising because changes in M affected the values of K, A_m, and maximum age nonlinearly (Table 1).

Changes in the M/K ratio did not reveal a clear trend (Tables 2 and 3, Fig. 5). As with M, the M/K ratio affects other parameters; therefore changes in M/K could be expected to produce a nonlinear response in the selection differentials. The percent selection differential on L_∞ was lowest at an intermediate value of $M/K=2$ (Table 3). The percent selection differentials on K showed no consistent trend (Table 2). For M/K values from 0.5 to 2.5, the selection differentials on size across ages ranged from 2.3% to 4.0% (Fig. 5).

Decreases in the spawning season duration (D_s) caused a near linear increase in the selection differentials (Tables 2 and 3, Fig. 5). A compressed spawning duration of one month resulted in a range of 5.0% to 7.4% selection differential on size across ages (Fig. 5). Of all the life-history parameters examined in this analysis, spawning duration had the greatest effect.

Fishery parameters

A limit (L_u) on sizes susceptible to the fishery decreased the selection differentials (Tables 2 and 3, Fig. 5). The percent selection differential at all ages was zero for $L_u = 800$ and –0.1% for $L_u = 700$ (Fig. 5). In these analyses, F was held constant. Consequently, smaller values of L_u correspond to fewer fish removed. An alternative approach would have been to maintain constant catch

Figure 4

Selection differentials on growth parameters (A) K and (B) L_∞, computed as functions of fishing mortality. Parameter values are the same as those in the base model.

by increasing F, which would have led to selection differentials larger than those in Tables 2 and 3.

Knife-edge selectivity ($\beta_s=\infty$) caused larger selection differentials than did selectivity curves with more gradual slopes (Tables 2 and 3). For β_s greater than 0.1, the selection differential rapidly converged to that of the knife-edge case (Fig. 5). As with L_u, F was held constant across β_s sensitivity analyses.

A change in the ages of fishery selectivity had little effect on selection differentials (Tables 2 and 3, Fig. 5). When selectivity was set to a larger age or size, the selection differential decreased slightly. In this case, selectivity was occurring after maturity, allowing more fish to reproduce before reaching sizes selected by the fishery. However if harvest had been held constant instead of F, the selection differentials would have been larger. When selectivity was set to a smaller age or size, the selection differential decreased slightly or remained constant. This result is due to a reduction in the time exposed to differential fishing mortality. Differential fishing mortality occurs only on the sizes where selectivity is less than one; otherwise fishing mortality is constant for all individuals. Under von Bertalanffy growth, younger fish grow more quickly. A decrease in the age or size of selectivity shifts the fishing pressure to ages with quicker growth, reducing the time

Table 3

Percent selection differential on the von Bertalanffy asymptotic length (L_∞) at fishing mortality = 0.8/yr. Columns correspond to the levels of the coefficient of variation (CV=0%, 10%, 20%) in L_∞ and in the growth coefficient (K). Any combination with 0% CV in L_∞ is not presented because it results in zero selection differential. The first row corresponds to the base model and subsequent rows correspond to changes in the base model: correlation between L_∞ and K (ρ), slope of maturity curve (β_m), natural mortality (M), M/K ratio, duration of annual spawning season (D_S), maximum size limit (L_u), slope of selectivity curve (β_s), change in age at 50% selectivity (A_s) in relation to the base case, and duration of annual fishing season (D_F).

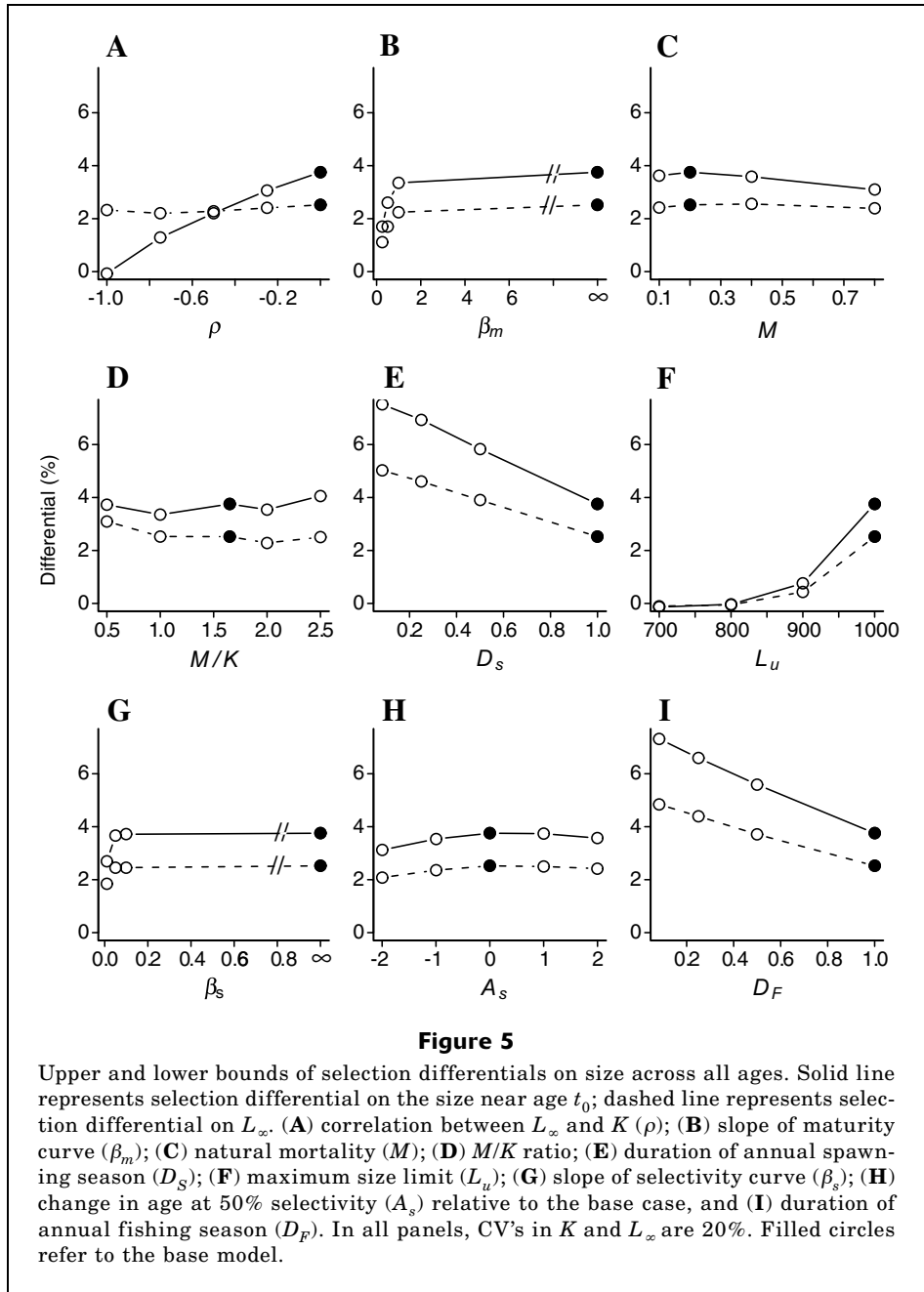|	Parameter values					
	L_∞: 0%CV K: 10%CV	L_∞: 10%CV K: 10%CV	L_∞: 20%CV K: 10%CV	L_∞: 0%CV K: 20%CV	L_∞:10%CV K: 20%CV	L_∞: 20%CV K: 20%CV
Base	1.0	2.7	0.9	2.7	0.8	2.5
$\rho = -1$	1.0	2.8	0.7	2.7	−0.1	2.3
$\rho = -0.75$	1.0	2.7	0.7	2.6	0.2	2.2
$\rho = -0.5$	1.0	2.8	0.8	2.7	0.4	2.3
$\rho = -0.25$	1.0	2.8	0.9	2.7	0.6	2.4
$\beta_m = 0.25$	0.3	1.2	0.3	1.1	0.3	1.1
$\beta_m = 0.5$	0.5	1.8	0.5	1.8	0.5	1.7
$\beta_m = 1$	0.8	2.4	0.7	2.4	0.7	2.2
$M = 0.1$	0.8	2.6	0.7	2.5	0.7	2.4
$M = 0.4$	1.0	2.8	1.0	2.7	0.8	2.6
$M = 0.8$	1.0	2.6	1.0	2.6	0.8	2.4
$M/K = 0.5$	1.4	3.2	1.4	3.2	1.3	3.1
$M/K = 1$	0.9	2.7	0.9	2.7	0.8	2.5
$M/K = 2$	0.9	2.5	0.8	2.5	0.7	2.3
$M/K = 2.5$	1.1	2.8	1.0	2.7	0.8	2.5
$D_S = 1/12$	2.2	5.6	2.0	5.5	1.7	5.0
$D_S = 3/12$	2.0	5.1	1.8	5.0	1.5	4.6
$D_S = 6/12$	1.6	4.4	1.5	4.3	1.3	3.9
$L_u = 700$	−0.1	−0.1	−0.1	−0.1	−0.1	−0.1
$L_u = 800$	0.0	−0.1	0.0	−0.1	−0.1	−0.1
$L_u = 900$	0.3	0.5	0.2	0.5	0.1	0.4
$\beta_s = 0.01$	0.5	1.9	0.5	1.9	0.5	1.8
$\beta_s = 0.05$	0.9	2.7	0.9	2.6	0.8	2.5
$\beta_s = 0.1$	1.0	2.7	0.9	2.7	0.8	2.5
$A_s = -2$	0.4	2.1	0.4	2.1	0.4	2.1
$A_s = -1$	0.7	2.5	0.7	2.5	0.7	2.4
$A_s = 1$	1.0	2.8	1.0	2.7	0.9	2.5
$A_s = 2$	1.0	2.7	0.9	2.6	0.8	2.4
$D_F = 1/12$	2.2	5.5	2.0	5.3	1.6	4.8
$D_F = 3/12$	1.9	4.9	1.7	4.8	1.5	4.4
$D_F = 6/12$	1.6	4.2	1.5	4.1	1.2	3.7

individuals experience differential fishing pressure and therefore the potential for selection differentials. If harvest had been held constant instead of F, the selection differentials would have been larger.

The fishing season duration (D_F) affected selection differentials in ways similar to the spawning season duration (Tables 2 and 3, Fig. 5). A fishing season of one month resulted in an upper bound of selection differentials that ranged from 4.8% to 7.3% over all ages (Fig. 5). Of all the fishery parameters examined in this analysis, a concentrated fishing season resulted in the largest selection differentials.

Discussion

The individual-based simulation approach used here simplifies computation of selection differentials and

Figure 5

Upper and lower bounds of selection differentials on size across all ages. Solid line represents selection differential on the size near age t_0; dashed line represents selection differential on L_∞. (**A**) correlation between L_∞ and K (ρ); (**B**) slope of maturity curve (β_m); (**C**) natural mortality (M); (**D**) M/K ratio; (**E**) duration of annual spawning season (D_S); (**F**) maximum size limit (L_u); (**G**) slope of selectivity curve (β_s); (**H**) change in age at 50% selectivity (A_s) relative to the base case, and (**I**) duration of annual fishing season (D_F). In all panels, CV's in K and L_∞ are 20%. Filled circles refer to the base model.

isolates the cause—fishing. Yet with any simulation analysis, one must interpret results in light of model assumptions. With our model maturity was assumed to be a function of age, and the computation of selection differentials were consequently focused to those on growth traits and size. If maturity were considered a function of size, it too would have been subject to a selection differential. Changes in size or age at maturity have been considered in other studies (Stokes and Blythe, 1993; Haugen and Vøllestad, 2001; Olsen et al., 2004) and are likely connected to growth parameters through bioenergetic constraints.

A central assumption is that somatic growth follows the von Bertalanffy model. That model was chosen because of its successful track record (Chen et al., 1992; Quinn and Deriso, 1999). Life-history characteristics other than growth are assumed to follow life-history invariant relationships. The invariants constrain biological parameters to values that represent an "average stock." Of course, no stock is truly average, and therefore our sensitivity analyses incorporate considerable deviation from life-history invariants.

In our simulation, the largest selection differentials occurred when the spawning or fishing seasons were

compressed. We modeled fishing seasons at the beginning of the year and spawning seasons at the end of the year, and in a single-year simulation, the annual timing of the fishing and spawning seasons will affect selection differentials. For example, if the one-month fishing season had been modeled at the end of the year, the selection differential would be smaller because of the 11 months of spawning prior to fishing mortality. Over multiple years, however, the annual timing of the fishing and spawning seasons is less important than their duration and overlap.

Our model simulated selection differentials at the onset of a fishery. As a fishery progresses, selection differentials should decrease as life-history parameters shift in the direction of selection. A multiyear simulation of evolution would require knowledge or assumptions about heritability and trait distributions, both of which are likely to be dynamic. Even so, a short-term simulation, where selection differentials and heritability are assumed to be static, may be an informative approximation.

We simulated evolution of the base-model population, assuming a static heritability of 0.2 and selection differentials of 2.5% for L_∞ and 1.2% for K (values from Tables 2 and 3 with 20% CV's in both parameters). Two simulations were conducted with different values for fishing mortality. With $F = 4M$, five years of evolution led to a 9.0% decrease in the capacity of spawning biomass. With $F = M$, five years led to a 2.3% decrease.

With real fishery data it is often impossible to document conclusively that fishing causes a genetic change in growth. Any such change may be hard to measure, fall within the range of statistical variability due to sampling, or be masked by strong year classes. Selection for reduced growth may be compensated by density-dependent effects (for example, lower abundance leaving more resources for survivors to allocate towards growth). Even when a change can be demonstrated, fishing is just one potential explanation. Alternative explanations include environmentally driven evolution and reaction norms (i.e., phenotypic expressions of a genotype-environment interaction).

Nonetheless, size-selective fishing is widespread and often accompanies changes in somatic growth rates (Ricker, 1981; Harris and McGovern, 1997; Haugen and Vøllestad, 2001; Sinclair et al., 2002). Until recently, the question was whether fishing can cause changes in growth that are evolutionary, and the answer was "yes ... probably." The laboratory experiments of Conover and Munch (2002) removed any doubt. However, those experiments represented an extreme fishery in terms of its potential to inflict a selection differential: high F compressed in time (90% of population removed in one day), knife-edge selectivity, non-overlapping generations, and a population where all individuals are susceptible.

The goal of our study was to shed light on selection differentials created by fishing under realistic ranges of life-history and fishery characteristics. Understanding how life-history characteristics affect selection differen-

tials is important for identifying which stocks are most susceptible to evolution of growth traits. For example, susceptibility increases with compression of the spawning season. Fish species with compressed spawning seasons, such as many anadromous species, may be at higher risk of evolution from size-selective fisheries.

Understanding how fishery patterns affect selection differentials has direct management implications because it is the fishery parameters that can be controlled. For example, our results indicate that size-selective fisheries compressed in time are apt to cause high selection differentials. Managers should avoid "derby" style harvests, such as the annual Pacific herring sacroe fisheries, which are completed in only a few days. Other management strategies could reduce selection differentials, such as slot limits, reduction in the slope of selectivity curves, and partial selectivity after the age at maturity. However, because no size-selective fishing pattern can preclude some directional selection on growth, management by area closures may be the best option for avoiding fishery-induced evolution of growth traits.

As fishing technology improves, so does the ability to fully and rapidly exploit fish populations, and thus increase the potential for evolutionary responses. Still, when overfishing depletes a stock, low abundance is usually the paramount concern. With appropriate management, stock abundance may recover, but pre-fishing growth capacity may recover more slowly or not at all if genetic variation is lost. Given plausible heritabilities of growth traits, this analysis shows that under a wide variety of life-history and fishery characteristics, selection differentials are large enough to allow for rapid evolution.

Acknowledgments

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