

Harvest selection, genetic correlations, and evolutionary changes in recruitment: one less thing to worry about?¹

S.B. Munch, M.R. Walsh, and D.O. Conover

Abstract: Harvest selection may lead to detrimental evolutionary changes in exploited populations. Few studies have considered the indirect impacts that harvest selection may have arising through genetic correlations. Using data from a long-term fishing experiment on Atlantic silversides (*Menidia menidia*), we show that there are significant genetic correlations between adult length at harvest and several early life history characters known to influence recruitment success. Based on this analysis, we estimate the magnitude of the change in recruitment success that may arise indirectly from selection on adults. In contrast with studies of harvest selection on adult characteristics, we find the response of characters in the early life history to be relatively slow and that impacts on recruitment, if any, are likely to be driven by selective changes in fecundity.

Résumé : La sélection due à la récolte peut mener à des changements évolutifs nocifs dans les populations exploitées. Peu d'études ont examiné les effets indirects que la sélection due à la récolte peut avoir par le biais des corrélations génétiques. À l'aide de données provenant d'une expérience à long terme sur les capucettes (*Menidia menidia*), nous démontrons qu'il existe des corrélations génétiques significatives entre la longueur des adultes à la récolte et plusieurs caractéristiques des premières étapes du cycle biologique, caractéristiques connues pour influencer le succès du recrutement. À partir de cette analyse, nous estimons l'importance du changement dans le succès du recrutement qui peut survenir indirectement par la sélection faite sur les adultes. Contrairement aux études faites sur la sélection due à la récolte sur les caractéristiques adultes, nous trouvons que les réactions des caractères des premières étapes du cycle biologique sont relativement lentes et que les impacts sur le recrutement, s'il y en a, sont vraisemblablement causés par des changements sélectifs de la fécondité.

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Introduction

There is growing concern that the selective effects of harvest may lead to detrimental evolutionary changes in life history characters (e.g., see Stokes et al. 1993). This concern is well founded, given the magnitude and size-selective nature of fishing mortality (Hanson and Chouinard 1992; Kristiansen and Svasand 1998) and the rapid evolution of life histories in natural fish populations (Reznick et al. 1990; Haugen and Vøllestad 2001). Significant changes in size and age at maturity have been observed in several heavily exploited stocks (Rijnsdorp 1993; Rochet 1998; Grift et al. 2003). In addition, several species have shown significant decreases in size at age, attributed primarily to evolution in response to harvest (Ricker 1981; Harris and McGovern

1997; Sinclair et al. 2002b). Since harvest selection is typically directed at mature individuals, most studies of fisheries-induced adaptive change have focused on production traits of adults, such as size and age at maturity. The potential for harvest selection to affect traits expressed earlier in the life history remains largely unstudied.

Recruitment variability is the most important source of uncertainty in managing fish populations (MacKenzie 2000; Rothschild 2000). Nearly 90% of a cohort may be lost during early life stages. Recruitment success has been linked to egg size (Rijnsdorp and Vingerhoed 1994), larval size at hatch, and growth through larval (Pepin and Myers 1991; Pepin 1993; Houde 1997) and juvenile stages (Sogard 1997). Variation in these traits among individuals is largely thought to be determined by environmental variation (e.g., Houde

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1987). In addition to predation, food availability (e.g., Cushing 1990), larval transport (Dalley et al. 2002), and turbulence (Rothschild and Osborn 1988) are among the many environmental factors thought to influence recruitment success.

The genetic basis of characters expressed early in the life history of fishes is largely undocumented. Consequently, the potential for genetically based changes in recruitment success has thus far been ignored. We have recently shown that artificial selection on adult size resulted in nonrandom, genetically based changes in juvenile size at age (Conover and Munch 2002; Munch et al. 2004). Since mortality through the juvenile stage is size dependent, we might therefore expect harvest selection on adult size to cause genetically based changes in recruitment.

Here, we reanalyze data from a long-term selection experiment on Atlantic silversides (*Menidia menidia*) (Conover and Munch 2002; Walsh 2003; Munch et al. 2004) and show that there are significant genetic correlations among adult traits and several early life history characters known to influence recruitment success. We briefly review the literature on the size dependence of mortality during the egg, larval, and juvenile stages to construct a size-based model of survival. Using this model, we evaluate the magnitude of the changes in recruitment per egg that can be expected from the selective removal of adults.

Methods

To estimate the expected change in recruitment resulting from selection on adult size, we need two things. First, we must have a means of estimating the expected change in early life history characters resulting from selection on adults. The experimental design described below provides information on genetic variance of, and covariance with, length at harvest. Using these data to estimate heritability and co-heritability (see Analysis and modeling section), we may make predictions of the evolutionary response of early life history traits to a single generation of selection on adult length. Second, we must have a model representing mortality as a function of each of the early life history characters that we measured. To this end, we reviewed the literature on survival as a function of egg diameter and length in larvae and juveniles.

Selection responses of correlated characters

To evaluate the selective effects of harvest on adult size and correlated life history characters, we conducted a long-term selection experiment using Atlantic silversides. The Atlantic silverside is a small, shallow-water atherinid found in estuaries throughout the eastern coast of North America from Florida, USA, to New Brunswick, Canada. Silversides have a simple annual life cycle: at all latitudes, all fish in wild populations mature at age 1 and are locked into doing so by the annual sequence in photoperiod. Given this constraint on silverside life history, our selection experiment focused on fishery-induced changes in size at age rather than age at maturity. Detailed descriptions of the design and primary results of the selection experiment have been published elsewhere (Conover and Munch 2002) and are only briefly reviewed here.

We established three kinds of experimental fisheries: (i) those in which only the largest fish were taken (largest 90% harvested), (ii) those in which only the smallest fish were taken (smallest 90% harvested), and (iii) those in which the fish were removed from the population randomly with respect to size (90% randomly harvested). Each of these experimental fisheries was replicated twice for a total of six independent experimental lines. To prevent loss in case of disease outbreak or system failure, we reared fish for each line in two independent, duplicate phases of approximately 500 fish each. Harvest occurred at the adult stage (190 days postfertilization) approximately 1 month prior to spawning. Each fishery was carried out for a period of five generations.

Recruitment in each phase of this experimental fishery was standardized in two stages. Initially, eggs deposited on spawning mops over a 1- to 3-day period were transferred into and allowed to hatch in rearing containers. On about day 30, after the initial larval mortality had subsided, 175 larvae from each of four to six birthdates spanning 1–2 weeks were transferred into rearing buckets. These 2-week birthdate intervals for each phase were taken from approximately the middle of the spawning period to ensure maturation of all potential spawners. A second density reduction occurred at 90 days of age when 550 juveniles, sampled uniformly from the rearing buckets, were transferred into larger aquaria for the remainder of the life cycle. Care was taken at both of these culling stages to ensure that the counting process was not size selective. Thus, recruitment for each population consisted of about 1000 fish at the time of harvest.

Some readers may question the adequacy of this experimental design as a simulation of fishing in wild populations. We acknowledge that the experiment differs significantly from real fisheries in several regards. First, recruitment is standardized. Consequently, density-dependent effects could have occurred only in the egg and early larval period and cannot be estimated from this design. Second, there are no predators. Consequently, apart from uncontrolled mortalities occurring from unknown causes, there is no natural selection acting to oppose the selection regime imposed by harvest. However, these apparent shortcomings are, in fact, the controls that allow us to accurately disentangle genetic from environmental influences on growth and other characters. As an experiment to estimate realized heritability for size at age, this experimental design is nearly ideal (Falconer and Mackay 1996). Finally, although it is expected that growth in the field may be quite different from that observed under laboratory conditions, it is the heritability of size, i.e., the fraction of variation in size attributable to additive genetic effects (see Analysis and modeling section), rather than size per se that is important. Estimates of the heritability of similar life history characters do not differ significantly between the laboratory and field (Weigensberg and Roff 1996).

Egg size, larval size at hatch, and larval survival were also measured. Egg diameters were measured for generations 3 through 5 on random samples of 30 eggs per experimental fishery (Walsh 2003). Larval size at hatch (total length) was measured for thirty 1-day-old larvae from each fishery in generations 4 and 5 (Walsh 2003). For the first generation prior to selection and generations 2 through 4, length at age 15 days was measured for 40–50 individuals from each fishery. All eggs and larval lengths were measured by ocular mi-

rometer (nearest 0.01 mm). Juvenile length at age was measured (nearest millimetre) every 20 days from age 90 to 190 days for fish in generations 3 through 5 on groups of 40–70 individuals sampled from each line (Conover and Munch 2002).

Posthatch larval survivorship was estimated on three batches of 50 larvae per experimental fishery (generation 5) fed ad libitum for 10 days posthatch (Walsh 2003). From these data, larval viability was calculated as $-\ln(N_{\text{final}}/N_{\text{initial}})/10$.

Analysis and modeling

Our experimental design provides information on the genetic variance of and covariance with adult length (i.e., length at 190 days) from which we may make predictions of the evolutionary response of early life history traits to a single generation of selection on adult length. Heritability (h_x^2) is defined as the expected change in mean phenotype of offspring in response to a unit of selection applied to parents (Fig. 1). In other words, it is the fraction of a change in the mean phenotype of parents that will be transmitted to offspring and may be estimated as the slope of the regression of offspring phenotype on parent phenotype. More formally, the response of a trait to selection is given by the breeder's equation

$$(1) \quad \Delta R_x = h_x^2 \Delta S_x$$

where the response to selection (ΔR_x) is defined as the observed difference between the mean offspring phenotype for trait x and that of the entire prior generation, while the selection differential (ΔS_x) is defined as the difference in mean phenotype of parents (i.e., the subset of the prior generation allowed to reproduce) and that of the entire prior generation.

Similarly, coheritability ($h_{x,y}$) is proportional to the additive genetic covariance among traits and, as the name implies, is related to the expected change in a trait that results from selection on another trait. As above, coheritability may be estimated as the slope of the regression of offspring phenotype on parent phenotype for another trait. (Here, we depart slightly from the definition for coheritability given in Falconer and Mackay (1996) to simplify the notation.) Formally, the change in a trait (y) resulting from selection on trait x is given by

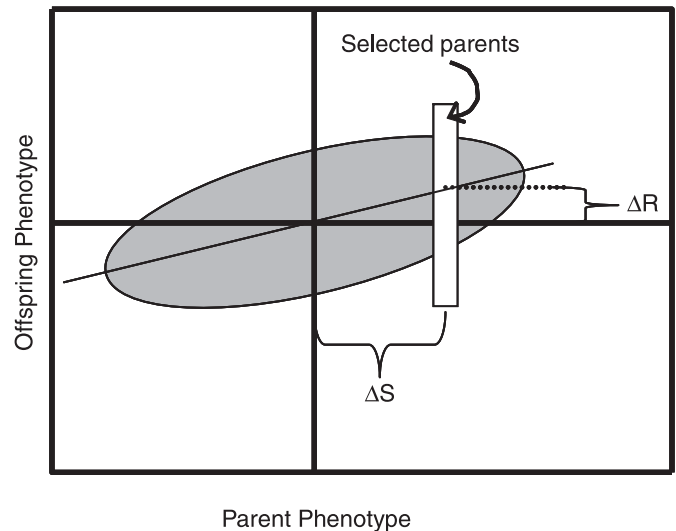
$$(2) \quad \Delta R_y = h_{x,y} \Delta S_x$$

Heritability and coheritability may be also estimated from selection experiments conducted over several generations (Falconer and Mackay 1996). In this case, the estimates are referred to as realized heritability and realized coheritability to distinguish them from their single-generation counterparts. Realized heritability (coheritability) is estimated by linear regression of the response to selection (as defined previously) on the cumulative selection differential. The cumulative selection differential at generation n ($\Delta S_{c,n}$) is defined as the sum of the single-generation selection differentials applied up to the present:

$$(3) \quad \Delta S_{c,n} = \sum_{i=1}^n \Delta S_{x,i}$$

To account for variance due to drift and unintended changes in the environment, we used a general linear model

Fig. 1. Heritability illustrated. The ellipse indicates the bivariate distribution of parent and offspring phenotypes. The slope of the regression line passing through this distribution is the heritability (h^2) or the fraction of a change in parent mean expected to be transmitted to offspring. The line gives the mean phenotypes of parents and offspring in the absence of selection. The rectangle indicates the range of parent phenotypes allowed to reproduce in a putative selection experiment. ΔS is the selection differential or difference in mean between selected and unselected parents. The expected change in the mean offspring phenotype is indicated by ΔR and is given by the breeder's equation $\Delta R = h^2 \Delta S$.



approach as follows. The vector of offspring mean length at harvest (L_{190}) for each line at each generation was modeled as

$$(4) \quad L_{190} = \mu + \beta \mathbf{X} + h_{190}^2 \Delta S_{c,n} + \epsilon$$

where μ is the mean, h_{190}^2 is the heritability of length at 190 days of age, $\Delta S_{c,n}$ is the vector of cumulative selection differentials, and ϵ is a normally distributed error term accounting for drift variance, measurement error, and non-additive genetic effects (see Falconer and Mackay (1996) for more details). Here, \mathbf{X} is a design matrix accounting for the effects of generation and phase. Specifically, the generation effect is simply a deviation from the grand mean common to all lines within a given generation. Similarly, the phase effect is a deviation from the generation mean common to all lines within a specific rearing phase. Thus, with the inclusion of the term $\mu + \beta \mathbf{X}$, eq. 4 is equivalent to an analysis of covariance (in which cumulative selection is the covariate) with phases nested within generations (McCulloch and Searle 2001). Coheritabilities were also estimated using eq. 4, by replacing L_{190} with vectors of mean egg diameter, larval viability, and length at age and modifying the design matrix to include only those generations and phases for which these traits were measured.

To predict changes in the size trajectory at ages other than those explicitly measured, we need an estimate of the coheritability function $h(L_{190}, L_t)$. Here, L_{190} is length at 190 days and L_t is length at some prior age (t). An estimate of the coheritability function may be obtained by fitting a

smooth function to the individual coheritability estimates (Kirkpatrick and Lofsvold 1989):

$$(5) \quad h(L_{190}, L_t) = h^2 \exp[-p_1(190-t)^2 - p_2(190-t)]$$

where h^2 , p_1 , and p_2 are coefficients that we estimated by nonlinear least squares from the coheritability values for each age, assuming additive normal errors.

We define recruitment per egg as survival from egg to age at harvest (190 days) and divide the life history into two distinct mortality stages, egg and larval-juvenile. In both stages, we model relative survival, defined as survival after a single generation of selection applied to adults divided by survival in the absence of selection. We assume that mortality through the egg stage declines exponentially with egg diameter (D) and is constant from fertilization until hatch. Parameters are drawn from Rijnsdorp and Vingerhoed (1994). Note that these parameters are for sole and may not apply directly to *M. menidia*. To our knowledge, however, estimates of the size dependence of egg mortality for *Menidia* or closely related species are unavailable. Rijnsdorp and Vingerhoed (1994) modeled mortality as $\ln M = a + bD + cT$ and reported values of $a = -0.075 (\pm 0.611)$, $b = -2.016 (\pm 0.251)$, and $c = 0.173 (\pm 0.039)$. We assume that temperature (T) over the 7-day egg stage is constant at 15 °C, the temperature at which silversides begin spawning, and combine their parameters a and c to give

$$(6) \quad S = \exp[-m_e \exp(bD)t_h]$$

where S is survival through the egg stage, $\ln m_e = 2.52 \pm 0.85$ with a standard error of $S_a^2 + (15 \text{ SE})^2)^{1/2}$, $b = -2.016$, and t_h is the duration of the egg stage (age at hatch = 7 days). Note that the error estimate for m_e includes measurement and process uncertainties and is likely to be considerably larger than an interval estimate based on process errors alone.

As described above, the change in egg diameter resulting from a selective change in length at harvest is given by $\Delta D = h(L_{190}, D)\Delta L_{190}$. Consequently, survival through the egg stage after selection, expressed as a fraction of survival in the absence of selection, is given by

$$(7) \quad S_E = \exp[m_e t_h (\exp(-bD) - \exp\{-b[D + h(L_{190}, D)\Delta L_{190}]\})]$$

Recruitment is also affected by changes in larval viability as assayed by the larval survival experiments. The viability mortality rate V resulting from selection on adults is given by $V = \bar{V} + h(L_{190}, V)\Delta L_{190}$ where \bar{V} is the mean mortality rate for an unselected population. Consequently, changes in viability, S_V , resulting from selection were modeled as

$$(8) \quad S_V = \exp[-h(L_{190}, V)\Delta L_{190}t_1]$$

where t_1 is the duration of the larval period and is assumed constant at 10 days. Note that the mean viability cancels when calculating relative survival so that S_V is insensitive to uncertainty in the mean mortality rate.

Survival from hatching to harvest is, in part, length dependent. Specifically, we consider mortality through the growing season as a sum of length-dependent and length-independent components. Assuming that the components of mortality that do not depend on length are the same for se-

lected and unselected populations, this additional mortality will cancel in the calculation of relative survival and can, for present purposes, be ignored. Based on our review of the literature, the length dependence of mortality during the larval and juvenile stages is modeled as a power function of length. Thus, the component of survival from hatching to harvest that depends on length is given by

$$(9) \quad S = \exp\left(-m_j \int_{t_h}^{t_r} L_t^d dt\right)$$

where t_r is the age at recruitment, held constant at 190 days. Here, L_t is the mean size at time t in the absence of selection for ages t_h to t_r . Since there are no adequate field estimates of silverside mortality as a function of length, the parameters m_j and d were estimated by linear regression of values of $\ln M$ on $\ln L$ (Fig. 2) obtained from Rilling and Houde (1999), Palomera and Leonart (1989), Pertierra (1992), Crecco et al. (1983), Dey (1981), and sources cited in Adams et al. (1996). Parameters for the length dependence of mortality for larvae and juveniles were $\ln m_j = 0.478 (\pm 0.636)$ and $d = -1.125 (\pm 0.203)$. Since these estimates are based on a regression of point estimates for a variety of species, the error bounds incorporate process uncertainty, measurement errors, and variation among species. The error bounds are thus likely to be substantially greater than a *Menidia*-specific process error interval and, within these bounds, our results for length-dependent mortality should be fairly robust. The L_t in the absence of selection was estimated as a second-order polynomial from the mean growth trajectories of fish in the random harvest lines in generations 3 through 5. Specifically

$$(10) \quad L_t = 0.002t^2 + 0.047t + 4.631$$

which describes the mean growth trajectory of unselected silversides quite well ($R^2 = 0.99$). Changes in length at age resulting from selection on adults were given by the coheritability function as $\Delta L_t = h(L_{190}, L_t)\Delta L_{190}$. Consequently, the relative survival S_J is given by

$$(11) \quad S_J = \exp\left(-m_j \int_{t_h}^{t_r} L_t^d - [L_t + h(L_{190}, L_t)\Delta L_{190}]^d dt\right)$$

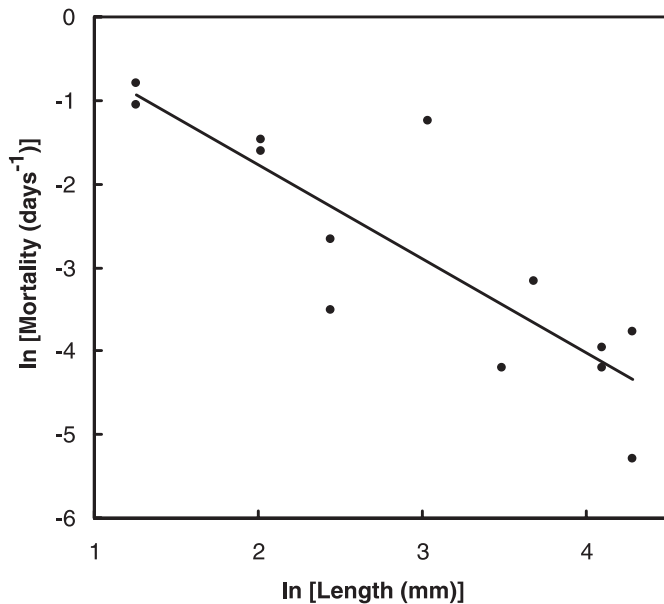
This integral was evaluated numerically using a daily time step over the period t_h to t_r .

The overall recruitment per egg (S_T) resulting from a round of selection on adults expressed as a fraction of recruitment in the absence of selection is given by

$$(12) \quad S_T = S_E S_V S_J$$

We modeled the relative survival of each stage using several different selection differentials. We used a selection differential of 10 mm, comparable with what was applied in our harvest selection experiment. We also used several values closer to those observed in actual fisheries. Law and Rowell (1993) estimated selection differentials for age-1 North Sea cod on the order of about -0.24 cm over a 3-month period or about -0.99 cm annually. Expressed in standard deviation units, this is equivalent to a standardized selection differential of -0.19 .

Fig. 2. Published values of $\ln(\text{mortality})$ versus $\ln(\text{length})$ for larvae and juveniles. This figure includes values from Rilling and Houde (1999), Palomera and Leonart (1989), Pertierra (1992), Crecco et al. (1983), Dey (1981), and sources cited in Adams et al. (1996).



Since the phenotypic standard deviation for length at harvest in *M. menidia* is 8.25, a selection differential comparable in magnitude with that of the cod fishery would be -1.6 mm. Relative survival was also assessed for selection differentials of 1, 2, and 3 mm. Sensitivity to the parameter estimates used in modeling was assessed by calculating relative survival using the upper and lower confidence bounds for each of the mortality parameters.

Results

Correlated characters

Selection on length at 190 days resulted in significant changes in egg diameter and larval viability (Walsh 2003). There were also significant changes in length at all ages (Table 1) (Conover and Munch 2002; Walsh 2003). In each case, the offspring of large-size harvested lines were smaller or less viable than offspring of the random- and small-size harvested lines. Curiously, lengths of larvae at age 15 days showed the opposite pattern; the large-size harvested lines were somewhat larger, although the differences were not significant. We expect that the absence of significant coheritability at 15 days is a result of the relatively small sample size used at this stage rather than an intermediate period during which the genetic correlation with adult size is reversed. The estimated realized coheritability function was highly significant ($R^2 = 0.99$, $p < 0.001$) (Fig. 2) with parameters $h^2 = 0.183$ (± 0.005), $p_1 = 0.0001$ (± 0.00003), and $p_2 = 0.004$ (± 0.0020). Thus, selection applied to length at 190 days had significant effects on length at all ages, the magnitudes of which increased with age.

Realized coheritability for egg diameter was 0.0006 (± 0.00004) ($p < 0.0001$). Since egg diameter was signifi-

Table 1. Age-specific coheritability estimates based on the generalized linear model described in this study.

Age (days)	Coheritability with length at 190 days	R^2	p
7	0.004 (0.0008)	0.677	0.001
15	-0.005 (0.0030)	0.140	0.125
90	0.046 (0.0038)	0.901	<0.001
111	0.063 (0.0079)	0.795	<0.001
133	0.094 (0.0098)	0.853	<0.001
153	0.138 (0.0092)	0.933	<0.001
174	0.169 (0.0099)	0.947	<0.001
190	0.182 (0.0106)	0.913	<0.001

Note: The numbers in parentheses are standard errors for the regression coefficients.

cantly correlated with maternal length ($r = 0.84$, $p < 0.001$), an obvious question is whether the observed variation in egg diameter is simply an effect of maternal size. We addressed this issue by including the mean length of parents at 190 days as an additional covariate in the generalized linear model to estimate coheritability. Here, mean length of parents is simply the adult length (i.e., on day 190) of the fish that were allowed to spawn rather than the mean size of the entire population. The estimated effect of parent length on egg diameter was marginally nonsignificant (slope = 0.0005 ± 0.00023 , $p = 0.06$). More importantly, the estimate of coheritability remained highly significant ($p = 0.0003$), indicating that selection on adult size resulted in significant genetic changes in egg diameter independent of maternal size effects. There were no significant phenotypic correlations between mean parent length and other early life history characters. Further, there were no significant phenotypic correlations between egg diameter and any other early life history character, although the correlation between egg diameter and larval length at hatch was only marginally nonsignificant ($r = 0.54$, $p = 0.07$). Thus, differences among selected lines in early life history traits are a direct consequence of genetic correlations with adult size. Coheritability for larval viability (0.0009 ± 0.0004) was marginally nonsignificant ($p = 0.06$).

Effects on recruitment

We found that using the mean values of the mortality parameters resulted in negligible reductions in survival as a consequence of selection (Table 2). For all selection differentials applied, the expected survival through each of the stages was never less than 88% of that expected in the absence of selection. Selection on adult size produced the greatest decrease in survival through the egg stage. Approximate confidence intervals for relative survival through each stage were obtained from the confidence intervals for the mortality parameters. For a selection differential of -1.6 mm, comparable with that in the North Sea cod fishery, we found a lower bound on relative egg survival of 87% and relative survival through the larval–juvenile stages of 79%. For the selection differential applied to our simulated fishery (-10 mm), the lower bound estimates of relative survival through these stages were 43% and 22%, respectively.

Table 2. Relative survival estimates.

Selection differential (mm)	Standardized selection differential	Egg survival ratio	Viability survival ratio	Hatch to harvest survival ratio
-1.6	-0.19	0.981 (0.874, 0.997)	0.98	0.986 (0.787, 0.999)
-10	-1.21	0.886 (0.430, 0.984)	0.91	0.915 (0.220, 0.995)
-1	-0.12	0.988 (0.919, 0.998)	0.99	0.991 (0.861, 1.000)
-2	-0.24	0.976 (0.845, 0.997)	0.98	0.983 (0.741, 0.999)
-3	-0.36	0.965 (0.777, 0.995)	0.97	0.974 (0.638, 0.999)

Note: Columns 1 and 2 give the modeled selection differential and standardized selection differential. Columns 3–5 give the survival of offspring of selected parents through each stage relative to expected survival in the absence of selection. In columns 3 and 5, the numbers in parentheses are ranges based on the confidence intervals for the mortality parameters. As noted in the Methods, uncertainty in viability cancels in the calculation of the survival ratio.

Discussion

Recruitment studies typically focus on the characteristics of larvae and juveniles independent from the rest of the life history. Here, we have demonstrated that there are significant genetic correlations between adult length and several early life history characters known to influence recruitment. We found significant estimates of heritability for egg diameter, length at hatch, and length from ages 90 to 190 days. At least qualitatively, our estimated heritability function for length at age (Fig. 3) is quite similar to the appropriate cross section of the genetic covariance function estimated by Kirkpatrick (1993) for rainbow trout, implying that this pattern of genetic covariation among lengths at age is a general phenomenon.

One cause for concern in this type of analysis is that the results may be artifacts caused by maternal effects or phenotypic correlations that result simply from the amplification of early differences in growth. In the first case, we should expect to find that the traits in question are more strongly correlated with maternal length than the cumulative selection differential. However, of the traits measured, only egg size was significantly correlated with maternal length at 190 days. Moreover, we found that after statistically controlling for the influence of selection, this correlation was no longer significant. In the second case, we would expect that size at age would be more strongly correlated with egg size or size at hatch than with the cumulative selection differential. No significant correlations with egg diameter or hatch length and length at subsequent ages were found. Consequently, we conclude that there are genetic contributions to egg size, length at hatch, and length at subsequent ages that share genetic correlations with length at 190 days.

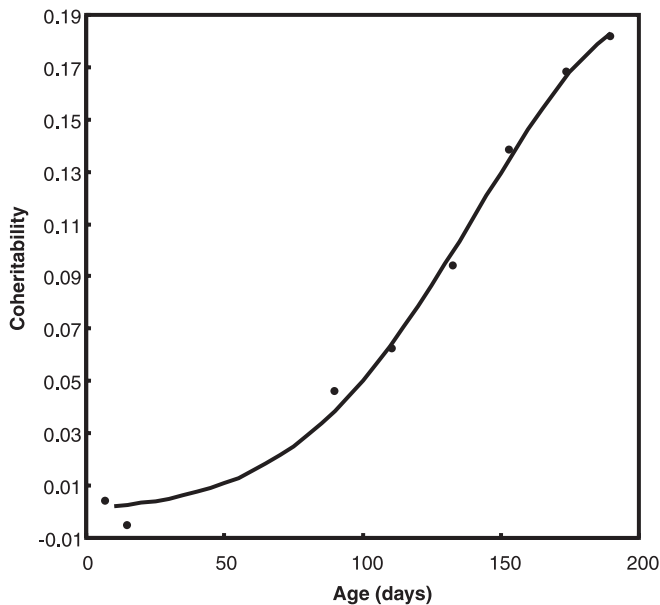
Based on our review of the mortality literature, we found that mortality appears to scale approximately inversely with length during the larval and juvenile periods. Several previous authors have reached similar conclusions regarding the length dependence of mortality (Petersen and Wroblewski 1984; McGurk 1986; Pepin 1993). Note that the size dependence exponent generated from data across several species (-1.125) is very close to those obtained by Lorenzen (1996) for mortality within species (mean -1.69 , range -0.6 to -5.21 , after excluding a single outlying value of -24.58 for *Stizostedion vitreum* from East Okerboji Lake). This suggests that the length allometry of mortality is fairly robust, although there may be considerable variation in mortality from other sources. Given that mortality is length dependent,

that growth through the larval stage is thought to be an important determinant of recruitment success, and that there are significant genetic correlations between sizes early and late in the life history, we expected to predict that selection on adult size would produce substantial changes in recruitment. However, our models revealed that despite significant genetic correlations between early life history characters and adult size, harvest selection is likely to have a negligible effect on recruitment per egg. This result is a consequence of two facts. The first is that the published selection differentials that are imposed by fisheries are fairly small (Law and Rowell 1993). The second is that the mortality and heritability functions have opposing trends that tend to negate each other. That is, fisheries-induced genetic changes in length are greatest just prior to harvest when length-dependent mortality is negligible and least during the larval stage when length-dependent mortality is the most severe.

It is important to note that our results apply only to a single generation of selection on adult length. We estimate that it would take at least five generations of selection (using average parameter values and a typical fishery selection differential of -1.6 mm) to cause a 20% drop in recruitment as a consequence of cumulative changes in survival through all stages. Considering each stage alone, it would take 12 generations of selection on adults to cause a 20% drop in egg survival and 15 generations to cause a drop of similar magnitude in survival through the larval–juvenile period. These estimates assume that there is no selection acting directly on these early life history characters that would oppose the correlated response from harvest selection and should therefore be considered a minimum bound on the number of generations required. Actual responses of early life history characters to harvest selection may be quite a bit slower.

Although the impacts of selection on recruitment per egg appear to be fairly mild for reasonable selection differentials, it is of interest to estimate the severity of selection required to achieve a given reduction in recruitment per egg. With this in mind, we have calculated the expected relative survivorship for a broad range of selection differentials (Fig. 4). Conveniently, we found that these predictions are well approximated by a simple exponential model, $S_T \approx \exp(r\Delta S)$. Here, ΔS is the selection differential expressed in standard deviation units and $r = 0.16$ for the mean model. Using the mean model, we found that to generate a 40% reduction in survival from egg to adulthood, selection would have to shift the mean length of survivors by more than 3 SD. Although it may well be that the selection differentials

Fig. 3. Realized coheritability function for length at age from hatch to harvest.

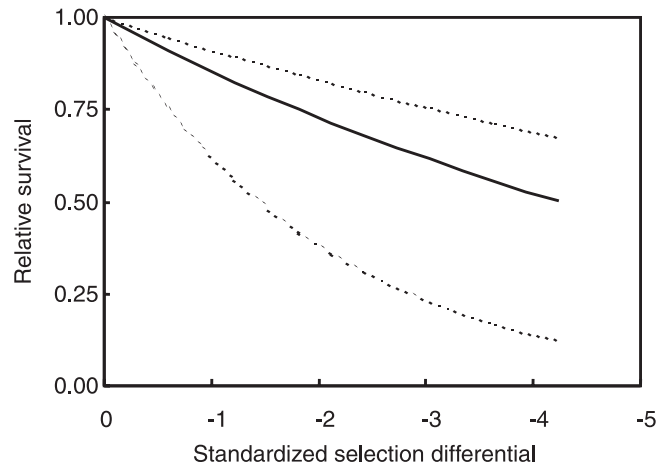


imposed by fisheries are more severe than current estimates indicate, selection of this magnitude is exceedingly unlikely. However, after incorporating uncertainty from the various submodels, the approximate confidence bounds are quite wide: $r = 0.09$ and 0.49 for the upper and lower bound models. When evaluated at the lower bound, a 40% reduction in survival requires only a decrease in the mean of 1 SD. The published literature on fishery-imposed selection differentials is quite limited and estimating selection differentials are an important area of research if the evolutionary impacts of harvest are to be managed. The methods applied by Sinclair et al. (2002a) represent an important step in this direction.

In modeling changes in recruitment per egg, we have made two simplifying assumptions. First, we assumed that coheritabilities measured in the laboratory might be reasonably applied to wild populations. To our knowledge, there are no studies comparing coheritabilities estimated in the laboratory and field. However, indirect support of this assumption comes from Weigensberg and Roff (1996), who have shown that estimates of heritability do not differ among wild and laboratory populations. Second, we compared survival for average growth trajectories of offspring from populations with and without harvest selection. Since size at age typically varies among individuals, a more exact, although computationally daunting, approach would involve integrating mortality through time over distributions of size at age. As long as selection differentials are small, our approach will be a reasonable approximation to the full stochastic model. If selection differentials are large and there is substantial variability in length, our approach will tend to overestimate relative survival, since there will be a much greater fraction of the selected population's length distribution that is subjected to high mortality.

Since our models focus on recruitment per egg, they do not address changes in recruitment due to selective differences in fecundity. Fecundity strongly depends on body size, and selective removal of large, old individuals may change

Fig. 4. Relative survival as a function of the selection differential. The horizontal axis in this figure is the reduction in mean length resulting from selection expressed in standard deviation units. The solid line shows the expected relative survival calculated as in eq. 12 for a broad range of selection differentials expressed in standard deviation units. The broken lines show the approximate confidence intervals based on upper and lower bounds for each of the mortality parameters.



population productivity (Rochet 2000). In fact, we observed changes in fecundity in our experimental populations. By generation 4, large-size harvested populations produced only half as many eggs as small-size harvested fish. While we do not have sufficient information to determine whether this effect is genetic or simply an effect of maternal size, this distinction is not entirely relevant. Since we expect that selection on adults will produce evolutionary changes in maternal size, changes in fecundity are expected to occur whether the positive correlation with maternal size is genetic or purely phenotypic. Since the total number of individuals recruiting to a population is given by the number of eggs produced and the probability that these will survive to adulthood, proportional changes in fecundity would, in the absence of density effects on survival, produce proportional changes in recruitment. Thus, a twofold change in fecundity would far outweigh any of the effects on recruitment modeled here.

It is also worth emphasizing that the traits that we analyzed here were measured under ideal laboratory conditions of unlimited food and we have not measured the responses of these traits to gradients in density. It is certainly possible that different growth and life history genotypes will be selected for under food-limiting conditions of high density (Sokolowski et al. 1997) and that this may alter the pattern of coheritability reported here. Consequently, our results will be most directly applicable to populations at low densities such as those recovering from exploitation. Viewed in this light, our experimental reductions in viability and modeled reductions in survival foreshadow corresponding reductions in the intrinsic rate of increase for heavily harvested populations and concomitant increases in the time required for population recovery.

There have been a number of recent studies modeling the adaptive response of fish populations to harvest selection. Owing to a lack of relevant data, few of these have at-

tempted to incorporate genetic covariance among traits. However, genetic covariance among traits may have important impacts on the response to selection, resulting in adaptive change along genetic lines of least resistance (Lande 1979). For instance, if there are strong genetic correlations among size at each age and selection during the early life history favors rapid growth, while harvest selection favors slow growth, size trajectories will evolve, but at rates lower than would be predicted for either trait alone. Consequently, the rates of evolution estimated using models of harvest selection that focus on single traits or ignore genetic correlations may be quite inaccurate. Given an estimate of the genetic covariance matrix, models like the ones we used may be generalized to include selective effects at other life stages (e.g., see Kirkpatrick (1993) for a description of the approach). Thus, an important next step in understanding the full life history implications of harvest selection is to estimate genetic covariances among life history characters (including growth trajectories) for exploited species.

This is the first paper to address the potential genetic impacts of selective fishing on early life history characters. We found that there were small but significant genetic changes in early life history characters that resulted from selection on adult size. In addition, although harvest selection appears to have substantial impacts on traits expressed in adults, our modeling results indicate that the expected response of early life history characters is much slower. Consequently, if significant changes in recruitment do result from harvest selection, our work suggests that they will be driven by changes in adult traits such as fecundity or age at maturity.

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