

LETTER

Maladaptive changes in multiple traits caused by fishing: impediments to population recovery

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Abstract

Some overharvested fish populations fail to recover even after considerable reductions in fishing pressure. The reasons are unclear but may involve genetic changes in life history traits that are detrimental to population growth when natural environmental factors prevail. We empirically modelled this process by subjecting populations of a harvested marine fish, the Atlantic silverside, to experimental size-biased fishing regimes over five generations and then measured correlated responses across multiple traits. Populations where large fish were selectively harvested (as in most fisheries) displayed substantial declines in fecundity, egg volume, larval size at hatch, larval viability, larval growth rates, food consumption rate and conversion efficiency, vertebral number, and willingness to forage. These genetically based changes in numerous traits generally reduce the capacity for population recovery.

Keywords

Biodiversity, conservation biology, correlated characters, exploited fisheries, life history evolution, overharvesting, size selection.

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INTRODUCTION

It is unclear why some collapsed fisheries fail to recover even after harvesting has been reduced for more than a decade (Hutchings 2000; Hutchings & Reynolds 2004). By targeting the oldest, largest, and fastest growing individuals in a stock, fisheries generate strong directional selection favouring the survival of younger, smaller, and slower growing phenotypes. Recent studies have shown that single traits such as body size, growth rate (Conover & Munch 2002), or age/size at maturity (Olsen *et al.* 2004) evolve rapidly in response to intense harvest mortality. Because of genetic correlations, however, selective removal of large fish is likely to also cause indirect changes in numerous other traits (Lande & Arnold 1983). Smaller adult body size, for example, may be correlated with earlier maturation, and reduced egg size (Trippel 1995), fecundity (Bobko & Berkeley 2003), larval growth and viability (Berkeley *et al.* 2004a,b). Such changes may accentuate the negative impacts of harvesting.

We conducted a harvest selection experiment on the Atlantic silverside (Pisces: Atherinidae), *Menidia menidia*, to assess the potential for genetic correlations to cause indirect changes in a variety of traits. We assayed a suite of

physiological, meristic, and behavioural characters that either directly or indirectly contribute to fitness, and consequently influence the rate at which overexploited populations may rebound.

The Atlantic silverside is a harvested marine fish commonly found along the east coast of North America (mean annual landings in New York, from 1996 to 2000, were 20.5 MT). This species possesses characteristics common to many marine fishes including external fertilization, small egg size, high fecundity, spawning *en masse*, pelagic larvae, and schooling behaviour. Yet the Atlantic silverside has an annual life cycle making it one of the few harvested marine vertebrates for which multi-generation selection experiments are feasible. Six captive populations of *M. menidia* were subjected to one of the following three harvesting strategies (two replicates per treatment): large-size harvest (largest 90% harvested), random-size harvest (90% of fish harvested randomly), and small-size harvest (smallest 90% harvested). After four generations of selection, the yield (biomass) from large-size harvested populations decreased twofold compared with that of small-size harvested stocks wherein yield had increased (Conover & Munch 2002). Changes in yield occurred because large-size harvested fish evolved a slower growth rate and smaller size

at harvest and vice-versa for small-size harvested populations. Using fish from the fifth generation of this experiment, here we demonstrate that harvesting the largest individuals caused substantial declines in egg size, larval size at hatching, rates of larval growth and viability, food consumption rates and growth efficiencies, willingness to forage under threat of predation, fecundity, and vertebral number.

METHODS

Harvest experiment protocol

To ensure adequate genetic variation in the founder populations, *c.* 700 wild adult *M. menidia* in spawning condition were collected from Great South Bay, NY, USA on 5 May 1998. Fish were transported to the Flax Pond Marine Laboratory, Old Field, NY, USA and divided evenly among two 1800-L tanks supplied with filtered natural seawater. Between 100 000 and 200 000 eggs from these two spawning groups were collected and pooled over a 2-day period. Each generation was reared under identical environmental and density conditions using previously published protocols (Conover & Present 1990). Food was provided *ad libitum* to allow genetic differences in growth to be fully expressed. In each generation, the six experimental populations were reared in two 'phases' consisting of groups of progeny from each treatment spawned separately over consecutive intervals each spanning 10–20 days of egg collection. The phases represented duplicates of each line that were reared in separate seawater systems as a precautionary measure in case of system failure or disease (neither occurred). Embryos were initially reared at 21 °C. Because *M. menidia* has temperature-dependent sex determination (Conover & Kynard 1981), larvae between 15 and 90 days old were reared at 15 °C to ensure a balanced sex ratio. Larval density was 175 per 19 L container. At 90 days, 550 juveniles from each phase and population were transferred to 700 L cylindrical tanks. Temperatures were then raised to 27 °C gradually over a 2-week period. When the average age of fish in each phase was 190 days, total lengths of all fish in that phase were individually recorded and sorted by size. The 90th (small-harvest populations) or 10th (large-harvest populations) percentiles of the size distributions were estimated and the appropriate harvest regime was then applied. In control lines, all individuals were also measured but then assigned randomly to either the harvested group or the spawning stock. The two phases of surviving fish within each population were then combined and photoperiod was altered to induce maturity. About 1.5 months later, eggs were collected from spawning tanks and reared as above, and so on for subsequent generations.

Statistical procedures

For all traits measured, differences between lines were examined using a two or three level-nested analysis of variance or covariance. The treatment effect (small, random, large-harvest), and replication (of lines nested within treatments) were the first two levels. A three-level nested ANOVA was necessary for egg volume and larval size at hatch because the date in which the trait was sampled was incorporated. When size varied, it was included as a covariate in ANCOVA.

Egg volume

Samples of 30 eggs per line were measured individually under a dissection scope. This procedure was performed six times.

Larval size at hatching

Hatch size was evaluated by measuring 30, 1-day-old larvae per population on five separate occasions. Failure to obey homogeneity of variances and normality necessitated the use of a Kruskal–Wallis test.

Larval viability

Three replicates, consisting of 50, 1-day-old larvae per line were stocked in 1-L containers. Larvae were fed *ad libitum* diets of brine shrimp nauplii and rotifers. After 10 days, the remaining living larvae were counted. This protocol was replicated for two separate dates of egg harvest. The data were arcsine transformed and the main effect mean squares were pooled as a result of a non-significant replication term.

Consumption rate and growth efficiency

Trials were conducted under unlimited and restricted ration conditions. The methodologies closely follow prior work (Present & Conover 1992; Billerbeck *et al.* 2000). For the unlimited food trial: three replicates of six fish per population were fed measured amounts of brine shrimp nauplii for 10 days at 23 °C. The initial lengths of the fish ranged from 18 to 20 mm. Each replicate was established from separate dates of egg harvest. Initial weights were determined by a previously established length–weight regression that consisted of 30 fish per treatment measured for length, wet weight, and dry weight. Nauplii were added, when necessary, to ensure *ad libitum* conditions.

After 10 days all fish were anaesthetized, and measured for total length, wet weight, and dry weight. Mean food consumption (mg day^{-1}) was calculated as: $(\text{food offered} - \text{food retrieved}) / (\text{number of fish} \times \text{number of days})$.

Growth efficiency (%) was estimated as the total increase in dry weight divided by the total dry weight consumption of brine shrimp. For the analysis of the unlimited food trial, mean squares were pooled because of a non-significant replication term.

In the restricted ration trial, all lines were given an equal, yet limited, ration. Three replicates of six size-matched fish (mean length from each population: 18 mm) were fed brine shrimp nauplii at a ration of 50% wet fish weight. The remainder of the procedure is the same as above.

Vertebral number

Radiographs of 100 fish per line were taken using a Hewlett-Packard Faxitron Series 43806 X-ray system (50 kVP, 6 mA, 60 s) (Hewlett-Packard Company, Palo Alto, CA, USA) on Kodak Industrex type M film (Eastman Kodak Company, Rochester, NY, USA). All X-rayed fish were 190 days old and were randomly chosen from the fish that were harvested in each treatment during generation five (mean total length: $L = 57.7$ mm, $R = 71.6$, $S = 81.7$). Differences in vertebral counts were analysed with log-linear models. Treatment, line replication, and vertebral number were the factors in the analysis.

Response to predators

The willingness to forage under the threat of predation was evaluated in fish from the large and small-size populations during generation 6. The time of emergence from an experimental shelter after a simulated predatory attack was evaluated. In each trial, five size-matched silversides (mean length 34.8 mm \pm 1.1 SD) were transferred to an experimental tank containing a small shelter. After an overnight acclimation period, all fish were chased with a model predator for 15 min until each individual consistently used the shelter to hide. Following another acclimation period (9 h), trials commenced by chasing the fish into the shelter for 15 min and food was then supplied via clear cylinders (1 m long, diameter 3 cm) placed at two corners of the tank. This procedure was replicated seven times.

Sigmoid curves were fitted to the trajectory of emerged individuals after the last chase in each trial, and the time (T_{50}) that 50% of individuals emerged was estimated. T_{50} were log-transformed to standardize variances and improve normality, and compared among treatments using a one-way ANOVA.

Swimming performance (U_{crit})

Trials consisted of six fish per treatment ranging from 18 to 22 mm. All protocols are based upon prior work (Billerbeck

et al. 2001). Twenty-four hours before each trial, fish were size-matched, isolated, and withheld from food. After transferring fish to the flume, trials began with a 15-min acclimation period at a slow flow speed (5–10 cm s⁻¹). Fish were then raised to their initial flow speed (13.5 cm s⁻¹) and raised one body length (2.25 cm s⁻¹) every 10 min. This stepwise increase occurred until all fish fatigued, defined here as failure to hold position and falling back upon the retaining screen. For each fish the time of failure and size were recorded. Exhaustion times were converted to critical speeds by the equation: $U_{crit} = V + (T/t \times v)$, where V is the highest speed maintained for a full time interval, v the velocity increment, T the time at failure, and t the time increment (Brett 1964).

RESULTS

Large-size harvesting caused significantly smaller egg volumes (Fig. 1a) and smaller larval size at hatching (Fig. 1b). In addition, estimates of coheritability between size at day 190, and egg size and size at hatch were both significant when maternal size was added as a covariate, indicating that selection on adult size has resulted in genetic changes in both larval traits irrespective of female size (Munch *et al.* 2005). Larval growth rates were also 25% lower in comparison with randomly selected controls [ANCOVA: $F_{(2,8)} = 5.44$, $P = 0.032$]. Furthermore, the probability of survival of these larvae to an age of 10 days was 61% lower than survival in randomly harvested lines (Fig. 1c).

Harvest selection on adult size caused significant declines in the consumption rates and growth efficiencies of juveniles in the large-size harvested lines. Under unlimited food conditions, the slow-growing, large-size harvested fish displayed significantly lower food consumption (Fig. 1d), and growth efficiency (Fig. 1e) when compared with randomly harvested lines. Additionally, even when all experimental fisheries were fed an equal but limited ration, the large-size harvested lines grew slower because of a 25% decrease in food conversion efficiency (Fig. 1f). Willingness to forage under threat of predation also evolved in response to fishing. When subjected to a simulated predatory attack, large-size harvested fish remained in hiding for a significantly longer period of time before resuming foraging (Fig. 1h).

Large changes in fecundity were observed. During generation 5, the fecundity in the large-size harvested populations was *c.* 60% less than the random-size harvested fish [eggs produced: large-harvest = 23 125; random-harvest = 64 250; small-harvest = 81 175; $F_{(2,3)} = 13.01$, $P = 0.033$]. As fecundity is nearly linear with length (Conover 1985), an approximate relative fecundity was calculated based upon the lengths of adults after selection.

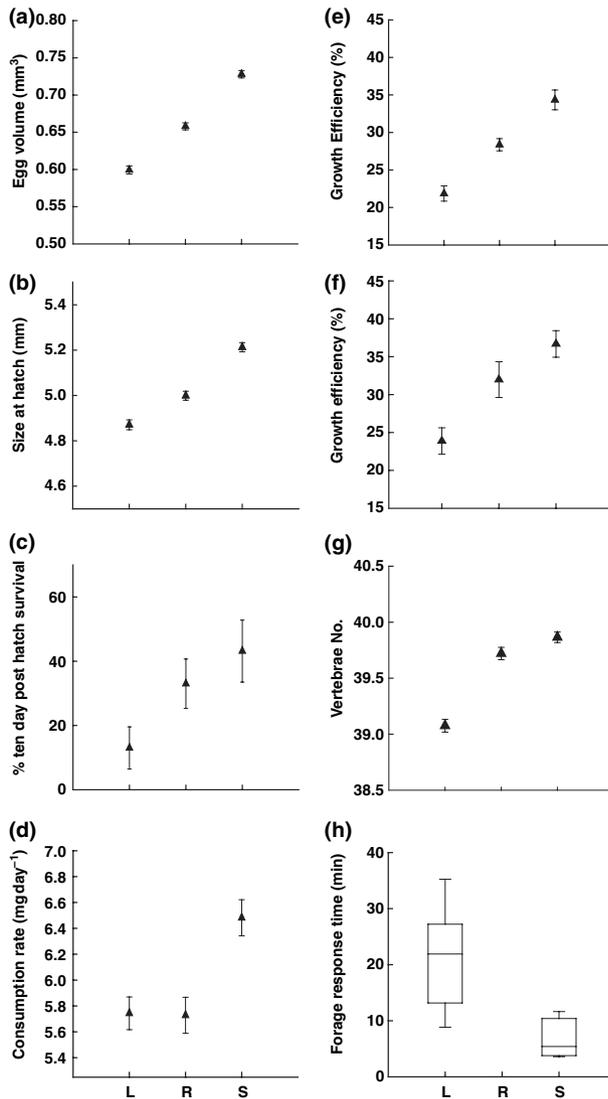


Figure 1 Correlated responses to harvest selection. Trends in egg volume (a) [ANOVA: $F_{(2,3)} = 55.87$, $P = 0.004$], larval size at hatch (b) [Kruskal–Wallis: $H_{(2)} = 117.62$, $P < 0.001$], larval viability (c) [ANOVA: $F_{(2,33)} = 3.614$, $P = 0.038$], consumption rate under unlimited food conditions (d) [ANCOVA: $F_{(2,14)} = 4.75$, $P = 0.027$], growth efficiency under unlimited food conditions (e) [ANCOVA: $F_{(2,14)} = 7.55$, $P = 0.006$], growth efficiency under restricted food conditions (f) [ANOVA: $F_{(2,3)} = 11.61$, $P = 0.039$], vertebral counts (g), and willingness to forage (h) [ANOVA: $F_{(1,12)} = 4.31$, $P = .014$]. L = large-size harvested lines, R = random-size harvested lines, and S = small-size harvested lines. Each datum is the mean of the two replicate populations per treatment. Error bars show ± 1 SE based upon variability among lines and replicates.

The relative fecundity of the large-size harvested fish was 66% (± 13) less than the random lines, while the relative fecundity of the small-size harvested fish was 47% (± 20) greater than the random treatments.

Vertebral number also evolved in response to harvest selection. The large-size harvested populations evolved a significantly lower number of vertebrae [Fig. 1g; $G = 61.126$; $P < 0.001$].

DISCUSSION

Fisheries theory assumes that harvest-induced reductions in population size will lead to increased per capita resources, and thereby increased fitness because of release from intraspecific competition (Grift *et al.* 2003). Implicit in fisheries theory, however, is the notion that changes in fitness are selectively neutral: no allowance is made for the possibility of evolution in response to harvest selection.

In marked contrast, our results demonstrate that a broad array of ecological functions spanning physiology, development, morphology, behaviour, and life history evolve in response to size-selective harvest. Early life history traits such as egg volume and larval size at hatch strongly influence survival. Given that larval mortality of marine fishes typically exceeds 99.9% (Houde 1987), and that the probability of survival is greatly enhanced by larger egg size (Rijnsdorp & Vingerhoed 1994), larval size at hatch, and faster growth (Pepin & Myers 1991; Pepin 1993; Houde 1997), slight reductions in these larval traits may have considerable consequences for recruitment to the juvenile stage. Decreased feeding rate, food conversion efficiency, and willingness to forage all reduce the per capita rate of energy flow and consequently reduce fitness. Finally, reductions in fecundity that occur as a consequence of smaller size will result in direct reductions in fitness.

Thus, despite the belief that increased food availability will increase productivity, we expect harvest selection to decrease the capacity for population recovery by decreasing traits that convert available energy into population growth. Such observations from wild harvested stocks are now accumulating (Sinclair *et al.* 2002; Barot *et al.* 2004).

In our experiment, we measured only a small subset of possible correlated traits. Based upon responses to selection in other taxa (Partridge *et al.* 1999; Garland *et al.* 2002; Rogers *et al.* 2005), it is likely that additional traits have evolved. For these reasons, the cascading effects of correlated responses may be far greater than are apparent from this study alone.

That fishing should cause maladaptive changes seems to defy a key principle of evolution. Should not selection favour genotypes with increased viability? The answer is yes, but under intense size-selective fishing, traits that would normally be favoured under natural conditions (e.g. fast growth, high feeding rates and large size) now reduce fitness. In essence, fishing warps the adaptive landscape by selecting against large size, which reduces the value of many correlated characters that ordinarily enhance fitness in unexploited

populations. Hence, when fishing pressure is lessened, the survivors are maladapted for an environment where only natural forces prevail. As a consequence, the capacity for population growth in these remnant fish is greatly reduced.

Another paradoxical result is that the small-size harvested fish displayed apparent increases in fitness compared with the controls (Fig. 1). Why were the wild founders of our captive populations not already displaying maximum fitness? The answer is that excessive growth can be detrimental because of trade-offs with other traits. Very fast growing silversides exhibit decreased swimming performance (Billerbeck *et al.* 2001; Munch & Conover 2004) and a higher susceptibility to predation (Lankford *et al.* 2001; Munch & Conover 2003). The founders of our experiment came from an intermediate latitude where selection favours a moderate rate of growth. This experiment demonstrates that small or large-size harvest can shift the balance of selection away from the local optimum.

Our results warn that evolutionary responses to harvesting will generally slow the recovery of over-exploited fisheries. Although some of this trait variation may represent phenotypic as opposed to genotypic correlations with size, declines in egg volume, larval size, and fecundity are important from a fishery management perspective regardless of the mechanism responsible. As long as variation in size has a genetic component, the syndrome of undesirable traits that are associated with small size will continue to adversely affect fisheries until large size becomes re-established in the population. How long that would take is unknown. However, because fishing mortality is typically far greater and more selective than natural mortality, the evolutionary reductions in size and correlated changes demonstrated here are likely to persist for some time, even after fishing is halted. We are currently investigating this by continuing our experimental populations with a reduced harvest regime.

Although precise predictions of the response to harvest selection will require a thorough understanding of the genetic covariance structure, some qualitative information about likely paths of evolution may be obtained from the pattern of local adaptation in the wild. Slow growing silversides from low latitude populations exhibit decreased consumption rates and growth efficiencies (Present & Conover 1992; Billerbeck *et al.* 2000), lower fecundity (Klahre 1997), and lower vertebral counts (Billerbeck *et al.* 1997) compared with high latitude conspecifics. Thus, the pattern of trait correlations that emerged in response to harvest selection mimics that observed among populations of silversides from different latitudes and demonstrates that the observed changes in large harvested fish are not likely experimental artefacts. This parallelism of genetic correlations within and among populations is common (Schluter 1996) and may be used to establish baselines for predicting evolutionary responses to harvest selection across stocks.

Commercially valuable species typically live for many years, have overlapping generations, and are harvested in a less precise manner than our experimental fisheries. As a consequence, similar responses in wild fisheries are unlikely to be as rapid. Yet evidence documenting phenotypic change for comparable traits in wild fisheries is accumulating (Rochet 1998). Moreover, selective breeding of economically valuable fish species for the purposes of aquaculture have repeatedly demonstrated that many of same traits measured in this study, including egg size (Gall & Neira 2004), fecundity (Su *et al.* 2002), consumption rate (Mambrini *et al.* 2004a), food conversion efficiency (Thodesen *et al.* 1999), and even feeding behaviour (Mambrini *et al.* 2004b) are also genetically correlated with size. Thus, we expect similar changes to occur in harvested populations, although at a rate commensurate with the generation time of the species in question and the intensity of selection imposed by the fishery.

Of perhaps greater importance are the reasons why some fish stocks fail to recover and others have proven to be quite resilient to exploitation (Hutchings 2000; Hutchings & Reynolds 2004; Hutchings & Baum 2005). We suggest that recovery time may be determined in part by the period and intensity of exploitation to which a population was historically exposed; prolonged exposure to intense selection would increase the likelihood of harvest-induced evolution and thus increase the time required for populations to recover. For example, Atlantic cod, has been harvested for at least 200 years, experienced genetically based declines in fitness related traits (Olsen *et al.* 2004), and exhibited a little rebound after considerable reductions in fishing. In contrast, similar species with shorter exploitation histories have rebounded in response to diminished harvesting (Hutchings & Baum 2005). This pattern, however, is merely suggestive, and more work is needed to clarify the disparate roles of harvest selection, life-history, community structure, and environmental forcing on the observed differences in recovery.

Many fitness correlates decreased as a result of harvesting the largest individuals in the population. These correlated responses could be indirect responses to a harvest-induced decline in maternal size or adaptive responses to the new fitness landscape. Regardless of the mechanism, they decrease the intrinsic capacity for the population to rebound under natural conditions. A new Darwinian fisheries paradigm is needed in order to account for such impediments to recovery and to ensure sustainable yields over evolutionary time scales.

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