PERSPECTIVE / PERSPECTIVE

Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*)[1]

David O. Conover, Stephen A. Arnott, Matthew R. Walsh, and Stephan B. Munch

Abstract: The potential of fishing mortality to cause rapid evolutionary changes in life history has received relatively little attention. By focusing only on ecological responses, standard fisheries theory and practice implicitly assume either that genetic influences on life history in the wild are negligible or that natural selection and adaptation is a slow process that can be effectively ignored. Lack of contrary evidence has allowed these assumptions to persist. Drawing upon >25 years of research on the Atlantic silverside (*Menidia menidia*), we show that adaptive genetic variation in many traits is finely tuned to natural variation in climate. Much of this variation is caused by a gradient in size-selective winter mortality and involves two- to threefold changes in physiological traits that influence population productivity. Many other species are now known to display similar patterns. Harvest experiments show that these traits can evolve rapidly in response to size-selective fishing. Hence, the pool of genotypes that code for life history traits is a highly dynamic property of populations. We argue that the lessons from *Menidia* are applicable to many exploited species where similar observations would be difficult to obtain and advocate greater use of species models to address fundamental questions in fishery science.

Résumé : On s'est peu intéressé à la possibilité que la mortalité due à la pêche puisse entraîner de rapides changements évolutifs dans le cycle biologique. En se concentrant seulement sur les effets écologiques, la théorie et la pratique courantes des pêches présument implicitement ou bien que les influences génétiques sur le cycle biologique en nature sont négligeables ou alors que la sélection naturelle et l'adaptation sont des processus lents qui peuvent en pratique être ignorés. Ces présuppositions ont pu se maintenir en l'absence de preuves contraires. En nous basant sur >25 ans de recherche sur la capucette, *Menidia menidia*, nous démontrons que la variation génétique adaptative de plusieurs caractéristiques est finement ajustée à la variation naturelle du climat. Une partie importante de cette variation est causée par un gradient de mortalité hivernale reliée à la taille et implique des changements de l'ordre de deux ou trois fois dans les caractéristiques physiologiques qui influencent la productivité de la population. Il est maintenant connu que plusieurs autres espèces possèdent des patterns semblables. Des récoltes expérimentales montrent que ces caractéristiques peuvent évoluer rapidement en réaction à la pêche sélective en fonction de la taille. Le pool des génotypes qui sont responsables des caractéristiques du cycle biologique forme donc une propriété très dynamique des populations. Nous croyons que les leçons apprises chez *Menidia* s'appliquent à de nombreuses espèces exploitées chez lesquelles des observations similaires seraient difficiles à faire et nous suggérons une utilisation plus grande en sciences halieutiques des modèles de population qui s'intéressent aux questions fondamentales.

[Traduit par la Rédaction]

D.O. Conover,[2] S.A. Arnott, and M.R. Walsh. Marine Sciences Research Center, Stony Brook University, Stony Brook, NY 11794-5000, USA.
S.B. Munch. Department of Applied Mathematics and Center for Stock Assessment Research, University of California, Santa Cruz, CA 95064, USA.

[1]This article was part of a special symposium entitled Building on Beverton's legacy: life history variation and fisheries management, which took place on 11–14 August 2003 in Québec, Quebec, during the 133rd annual meeting of the American Fisheries Society.
[2]Corresponding author (e-mail: dconover@notes.cc.sunysb.edu).

Introduction

Among the first to appreciate the importance of life history variation to fishery science was R.J.H. Beverton. Much of Beverton's work focused on explaining the incredible diversity of life histories in fishes. Some of his most important contributions were that fishery harvest regimes must be tailored to the differences in life history that occur among species or populations (Beverton and Holt 1957), that some life histories are far more susceptible to overfishing than others, and that life history traits are highly intercorrelated across species such that changes in one trait are predictably associated with changes in other traits (Beverton 1992). Beverton's attention was focused primarily on differences among species and populations because at these phylogenetic levels, phenotypic differences are likely to have a genetic component and therefore represent the result of evolutionary divergence rather than environmental influences alone.

The preeminence of the population and (or) species levels as the major sources of genetic variation relevant to fishery management still prevails. We recognize that populations of a species represent unique gene pools or "evolutionary significant units" that have a spatially explicit phylogeographic structure defined by the level of gene flow and within which may exist genetically based adaptations to local environmental conditions. Lineages must therefore be preserved, if threatened with extinction or introduction of alien genotypes, so as to protect the genetic diversity of a species. At the individual level, however, fishery management theory implicitly assumes that phenotypic variation is purely environmental. Essentially, we assume that the effect of harvest on a stock is analogous to mowing a lawn, i.e., removal of biomass stimulates new production for further harvest, without changing the intrinsic characteristics (i.e., the gene pool) of the lawn. But in reality, fishing is a sorting process that selectively removes individuals. Even though the importance of individual genotypic differences has long been recognized in fish breeding and hatchery operations, we have not fully appreciated the fact that genetic variation in nature is organized in a hierarchical fashion beginning first among individuals within populations, then among populations, and then among species. In short, we do not consider individual genotypes to be evolutionary significant units in managing fishery harvests.

Why have we largely ignored genotypic variation in life history in the wild as relevant to harvest management? We offer several reasons. First is the fact that physiological and life history traits are notoriously difficult to observe at the individual level. Unlike morphology or behavior, for example, which can be observed visually, physiological traits in the wild are essentially invisible to us. Instead, we measure physiological traits indirectly through analysis of aggregate measures such as change in mean size or proportion maturing at age. These practices often obscure individual variability. Second is the belief that phenotypic plasticity of physiology and life history at the individual level in nature is so high that genetic influences are easily swamped by environmental influences. Physiological traits like growth rate, for example, vary dramatically with environmental factors such as temperature. We therefore focus attention on extrinsic factors with the greatest apparent impact and, for the sake of simplicity, ignore the rest. For example, bioenergetics models designed to predict fish growth in response to environmental differences are routinely parameterized without regard to genetic differences below the species level, and in fact often borrow parameters across species (Munch and Conover 2002). Such practices assume that genetic effects on physiology at the individual or population level are weak relative to environmental influences and therefore can be safely ignored. Third is the belief that genetic adaptation is a slow process requiring time scales far longer than those of ecological processes. Hence, evolutionary responses to harvest mortality also can be effectively ignored and population dynamics can be modeled as a function of ecological density-dependent responses alone.

What if these premises are wrong? What if within populations there is substantial variation among genotypes that code for life history differences expressed by phenotypes that differ in their susceptibility to fishing, much like species do? What if local adaptation is a rapid process that can occur despite gene flow and on time scales relevant to contemporary management decisions? If so, then we would expect to see in the absence of fishing that adaptive traits are finely tuned to selective agents in nature, that the geography of adaptation is spatially coherent with strong environmental gradients, and that such traits are capable of responding rapidly to selection. In harvested stocks, we would expect to see shifts in life history parameters that reflect the change in fitness caused by the addition of fishing mortality to natural mortality.

In this essay, we address these questions by reviewing what has been learned about life history evolution from >25 years of research on a single model species: the Atlantic silverside (*Menidia menidia*). We first describe the ecology and life history of *M. menidia* in nature, focusing particularly on variation in growth across a latitudinal gradient, its physiological basis, and its adaptive significance. Then we use this knowledge to explain the design of, and interpret, an artificial selective harvest experiment. We evaluate the validity of *M. menidia* as a general model by extrapolation to and comparison with other species and fisheries. Finally, we argue that tractable biological models have an important place in fisheries science, particularly for difficult problems like teasing apart the genetic and environmental components of life history variation.

Seasonality and the evolution of countergradient growth variation in *M. menidia*

Like many marine fish species that inhabit nearshore waters along the east coast of North America, the Atlantic silverside has a broad latitudinal range, extending continuously from northern Florida to the Gulf of St. Lawrence. Its range crosses one of the steepest latitudinal temperature gradients in the world. Many elements of the ecology and life history of the Atlantic silverside are common to other marine species. *Menidia menidia* spawns in the spring in synchrony with full and new moons, releasing eggs of about 1 mm diameter that are broadcast with milt en masse by

732

Can. J. Fish. Aquat. Sci. Vol. 62, 2005

large schools of fish in the intertidal zone (Conover and Kynard 1984; Middaugh et al. 1984). Relative fecundity is exceedingly high, as batch spawning allows females to produce a cumulative egg mass roughly equivalent to their body mass over the breeding season (Conover 1985). Spawning occurs in salt marsh (*Spartina alternaflora*) environments that occur continuously along much of the North American east coast. Embryos attach to intertidal algae and *Spartina* without provision of postspawning parental care. Larvae hatch at about 5 mm in length and soon thereafter display schooling behavior that is maintained throughout life. Northern fishes migrate offshore to continental shelf waters in winter and return to the shore zone in spring (Conover and Murawski 1982). While it is possible that some degree of homing behavior may occur (this is currently being studied using otolith microchemistry), the species as a whole can essentially be thought of as a continuous distribution of subpopulations that can mix freely with nearest neighbors up and down the coast (Conover 1998, and see below). Where the life cycle of *M. menidia* departs greatly from that of other marine species is in age at maturity and longevity, which is 1 year for both traits throughout the species' range, although a few fish (generally <1%) reach age 2 at the northernmost latitudes (Conover and Ross 1982; Jessop 1983). Hence, silversides at all latitudes experience only one growing season before becoming an adult. This annual life cycle, and the ease with which it can be replicated in captivity, is what enables much of the research described below.

The Atlantic silverside provided the original discovery in fishes of temperature-dependent sex determination (TSD) (Conover and Kynard 1981). TSD is adaptive in *M. menidia* because it ensures that most fish produced at the beginning of the breeding season will become female, and it is female fitness that benefits more than male fitness from a longer growing season and thereby larger adult size (Conover 1984). To provide conclusive proof that TSD was adaptive, progeny from six locations representing different climates along the North American coast were reared at multiple identical temperatures. By standardizing the environment, such "common garden" experiments allow the genetic component of phenotypic differences among latitudes to be revealed. The results showed that the functional response of sex ratio to temperature differed greatly with latitude, proving that genetic adaptation existed (Conover and Heins 1987). Selection experiments on captive populations demonstrated that the functional relationship of sex ratio to temperature was capable of rapid evolution in response to climate change (Conover and Van Voorhees 1990). TSD is now known to occur in numerous species including commercially harvested and (or) cultivated species such as sockeye salmon (*Oncorhynchus nerka*), European sea bass (*Dicentrarchus labrax*), tilapia (*Oreochromis niloticus*), and several flatfishes (*Paralichthys* spp.) (Devlin and Nagahama 2002; Conover 2004). Only in the silverside, however, is the adaptive significance and evolvability of TSD understood, and this is principally because of the ease with which common garden experiments and selection experiments can be conducted with this species. Unexpectedly, these initial common garden experiments also provided evidence that many other characteristics of *M. menidia* differed genetically with latitude, especially those related to growth rate.

The Atlantic silverside displays a geographic pattern of variation in growth rate known as countergradient variation (CnGV) (Conover 1990; Conover and Present 1990). CnGV occurs when genotypes are distributed across an environmental gradient in nature such that genetic influences counteract environmental influences on a trait, thereby diminishing phenotypic variation (Conover and Schultz 1995). In the case of *M. menidia*, the capacity for growth (i.e., maximum rate expressed under unlimited rations) increases with latitude, thereby counteracting the decline in temperature and length of the growing season that would otherwise cause less growth in the north. The end result is that adult *M. menidia* are about the same size at all latitudes despite a threefold change in length of the growing season. Common garden experiments on progeny reared over multiple generations proved that the differences in growth rate are genetic (Conover and Present 1990). Because the genetic differences in growth are tightly correlated with latitude, they must be the result of selection rather than genetic drift.

What agents of selection might be responsible for CnGV in growth rate? A primary cause is the size dependency of winter mortality. Large fish survive the winter at higher rates than do smaller fish, and the severity and size dependence of winter mortality increase with latitude (Conover 1990; Schultz et al. 1998; Munch et al. 2003). Hence, with increasing latitude, the length of the growing season diminishes, while the necessity of large size increases, leading to increased selection for rapid growth in the north. But selection caused by winter mortality cannot be the complete explanation. Even in the absence of winter mortality, there are many other components of fitness that covary positively with size (e.g., fecundity, swimming performance, overall survival): why should low-latitude fish evolve submaximal rates of growth when higher rates are clearly possible? There must be trade-offs that cause balancing selection for submaximal growth.

To address this question, we investigated the physiological correlates of variation in growth rate. Northern genotypes grow faster by consuming more food and converting food more efficiently into somatic tissue while maintaining only a slightly higher routine metabolic rate (Present and Conover 1992; Billerbeck et al. 2000). Northern fish also store lipid reserves at higher concentrations prior to winter (Schultz and Conover 1997) and when spawning produce larger eggs at a higher rate with higher efficiency than do southern fish (Klahre 1998). Overall, bioenergetic model parameters for northern versus southern genotypes differed by an average of 28% (Munch and Conover 2002), clearly demonstrating the importance of accounting for intraspecific variation in physiology. In short, northern fish grow more rapidly than southern fish by adopting very high rates of energy acquisition and by allocating proportionately more of their acquired energy to tissue synthesis during the growing and spawning seasons.

Energy acquisition, digestion, and tissue synthesis are energetically expensive. In *M. menidia*, metabolic rate more than doubles after consuming a meal and is proportional to meal size (Billerbeck et al. 2000). Based on mass balance energy budgets, the trade-off with such high rates of investment in energy acquisition and tissue synthesis would likely involve activity. Recent experiments support this hypothesis.

Northern fish are inferior to those from the south in terms of both sustained and burst swimming speed (Billerbeck et al. 2001). Experiments on growth-manipulated phenotypes within each genotype provided evidence that differences in swimming performance are a function of differences in growth rather than other intrinsic characteristics. Moreover, the cost of growth in terms of reduced swimming performance accelerates greatly as maximum growth rates are approached (Munch and Conover 2004). Hence, the marginal cost of growth can be reduced by not exceeding intermediate rates of growth.

For Atlantic silversides, schooling and fleeing when attacked are the principal means of evading predators. Thus, swimming performance should be directly linked to predator escape performance. This prediction was supported by experimental trials comparing predation rates of fast- versus slow-growing genotypes and growth-manipulated phenotypes (Lankford et al. 2001). Slow-growing fish are less susceptible to predators at a given size than are fast-growing fish when comparing either northern versus southern genotypes or growth-manipulated phenotypes within genotypes. In addition, the mere act of consuming large meals causes an immediate decline in swimming performance and an increase in predation vulnerability (Billerbeck et al. 2001; Lankford et al. 2001). Although these trade-offs have yet to be tested in the field (research currently in progress), there appear to be substantial costs associated with both the means (consuming large meals) and the end result (a bigger but relatively slower body) of rapid growth.

These studies of *M. menidia* suggest that growth rate and many of the underlying physiological traits that covary with and influence growth rate are fine-tuned to selection gradients that exist in nature. Size-dependent sources of natural mortality play a key role in explaining these gradients. Maintenance of such strong countergradient patterns in growth suggests both sufficient heritability within populations and ongoing selection. The former is a general prerequisite for evolutionary divergence and the latter is necessary to explain why gene flow, which appears to be substantial (Conover 1998), does not homogenize genetic variation along the coast. Individual physiological traits such as food consumption rate, growth efficiency, and metabolism are the foundation of stock productivity at the population level. If these traits are heritable and fine-tuned to size-dependent sources of natural selection in the wild, then there is every reason to suspect that such traits would evolve in response to artificial sources of size-dependent mortality that may be imposed by harvesting. We used selection experiments to address these issues.

Life history evolution under size-selective harvest regimes

We designed a size-selective harvest experiment with several questions in mind. First, what are the rates at which growth rate would evolve under size-selective harvest and how rapidly would such changes affect the productivity of populations? Second, what changes would occur in other traits correlated with growth rate and would these covary in a fashion similar to that of wild Atlantic silversides from different latitudes? Could artificial size selection alone create genotypes with physiologies like those of northern and southern fish in the wild? Finally, what would happen to populations that evolved in response to size-selective harvest and then experienced a selective harvest moratorium? Is it possible for evolution to reverse course back to the original condition and, if so, at what rate? The first two sets of questions will be discussed below, while the third is the subject of ongoing investigation.

The experiment involved the establishment of six captive populations of 1100 *M. menidia* collected from an intermediate latitude (New York) so that the intrinsic growth rate potential was in the middle of the range found in the wild (Conover and Munch 2002). Larvae were initially assigned randomly to each of the six populations so that the initial gene pools of the populations would be homogeneous. As the fish in each population reached adult size (i.e., day 190), 90% harvest rates were imposed. Two populations were harvested based on a minimum size rule (the largest 90% were harvested), two populations were harvested based on a maximum size rule (the smallest 90% were harvested), and two populations were harvested randomly with respect to size. The survivors (about 100 fish per population after accounting for incidental mortality prior to harvest) were induced to spawn, and their offspring were reared and treated as described above.

After only four generations of size-selective harvest, the yield of the populations had changed dramatically (Conover and Munch 2002). Yield in large size harvested lines was initially higher than the others but declined. The yield in small size harvested lines was initially low but increased. By the fourth generation of selection, the yield of small size harvested populations was twice that of large size harvested populations. The reasons for the yield differences were clearly due to genetic changes in the mean growth rate of fish within populations during both the larval and juvenile stages. Hence, gradients in size-dependent mortality are capable of causing rapid evolution of growth rate and thereby provide a plausible explanation for CnGV in the wild. These results also raise obvious concerns about the long-term effects of size-dependent harvest regimes on the productivity of populations.

Similarities in the physiology of the artificially selected fast- and slow-growing genotypes with those from different latitudes strengthen our conclusion that gradients in size-selective mortality account for countergradient growth variation in the wild. Walsh (2003) demonstrated that fish from lines that evolved faster growth also displayed significantly higher rates of food consumption and growth efficiency than those from slow-growing lines. Moreover, the fish from slow-growing lines displayed about a 10% faster critical swimming speed than fast-growing fish, although the differences were not significant and need further study before definitive conclusions can be drawn. Nonetheless, the changes in physiology caused by selective harvest are qualitatively similar to those existing at different latitudes in the wild. This suggests that our selective harvest experiment is a reasonably accurate mimic of selective agents operating in nature. It also shows that size-selective mortality alters a whole suite of interrelated physiological characters. If the potential for evolution of physiology in *M. menidia* can be generalized to other species, then the Darwinian response to

harvest mortality clearly needs further attention by fisheries scientists.

Is *M. menidia* a valid model of general phenomena?

Our empirical simulation of the evolutionary effects of harvest has been criticized on the basis that harvest experiments on captive fish in controlled environments are not comparable with evolution in wild populations or in real fisheries. In the absence of knowledge about countergradient growth variation in the wild, this criticism would be highly appropriate, and there is always concern about the realism of any model, be it mathematical, statistical, or empirical. However, the harvest experiment was motivated specifically from detailed knowledge of natural variation in growth and its physiological correlates in response to a naturally occurring gradient in size-selective mortality. At least with respect to *M. menidia*, there appears little doubt that size-selective mortality in the wild exerts major influences on physiology and life history over contemporary time scales.

The question remains, however, whether or not the evolvability of life history traits and the magnitude of local adaptation are idiosyncratic in *M. menidia*. The rate at which a trait will evolve is a product of the heritability of phenotypic variation within a lineage or group (i.e., the proportion of phenotypic variance transmitted from parents to progeny) and the selection differential (i.e., the change in the trait mean that results from selection prior to reproduction) applied to that lineage. This fundamental identity of quantitative genetics is known as the breeder's equation. High heritability of traits coupled with large selection differentials would cause rapid evolution. Low heritability and moderate selection differentials would cause slow evolutionary change. Assuming at least moderate heritability, the potential for local adaptation in the wild is therefore determined by the change in selection differentials across environments. It is also influenced by the level of gene flow across environments. Large changes in the fitness of phenotypes combined with low gene flow across environments would lead to high levels of local adaptation. On the other hand, high gene flow across environments could swamp the effects of differential selection. If *M. menidia* is unusual in any of these characteristics, for example by displaying unusually high heritability for growth or fine-scaled spatial isolation of populations along the coast, then patterns observed in this taxon may not be general.

Available evidence would suggest, however, that these attributes in *M. menidia* are like those of numerous other marine species. The heritability for growth rate in *M. menidia* is about 0.2 (Conover and Munch 2002), a value similar to those observed for life history traits in many organisms including fishes (Roff 2002). Hence, the potential for evolution of growth-related traits within a population is not unusually high in *Menidia*. It should be pointed out that this heritability value applies strictly to the founders of the selection experiment, which were collected from New York. More northern or southern groups may have higher or lower growth rate heritability and therefore a different potential for evolution. Hence, at least for silversides from New York, the experiment demonstrates that there is sufficient genotypic variation in growth rate within extant populations to allow evolution, but not exceptionally so.

Menidia menidia is also not unique with respect to gene flow among populations. The level of gene flow is indexed by the geographic structure of genetic variation neutral to selection. High levels of genetic structure are found in species with highly isolated populations. Studies of population structure based on neutral molecular markers reveal that the proportion of total genetic variation attributed to populations in *Menidia* is low: i.e., on the order of about 1%–3% (Conover 1998), which is typical of marine species with dispersive life stages that lack barriers to gene flow. Hence, the evolvability and potential for local adaptation of physiological traits in *M. menidia* are not remarkable.

The annual life cycle of the Atlantic silverside is unique among temperate marine species of the western North Atlantic, and it belongs to a taxonomic family (Atherinidae) and order (Atheriniformes) in which relatively few long-lived, economically valuable species are found. Do the unique life history characteristics (nonoverlapping generations, lack of age structure) and taxonomic affinities of *M. menidia* limit its usefulness as a general model for fishes? The answer appears to be no. First, the existence of TSD, as first reported in *M. menidia*, has now been confirmed in numerous other species from many taxons and with highly divergent life histories, including over 50 fish species from 18 genera representing seven orders (reviewed in Devlin and Nagahama 2002; Conover 2004). Knowledge of TSD is crucial in development of methods for manipulating sex ratio in the aquaculture industry and in stock enhancement efforts where hatchery-reared fish are planted in the wild. Second, several long-lived, harvested species that inhabit eastern North America also appear to display CnGV in growth (Conover 1990). In striped bass (*Morone saxatilis*), for example, the parallels with *M. menidia* are clear. Striped bass sizes at the end of the first growing season are similar across latitudes (Conover 1990), size-dependent winter survival selects for larger young-of-the-year at northern latitudes (Hurst and Conover 1998), and experimental evidence from common garden experiments confirms that the capacity for growth increases with latitude (Conover et al. 1997). Evidence of CnGV in growth has also been found in numerous and phylogenetically diverse fishes including Atlantic halibut (*Hippoglossus hippoglossus*) (Jonassen et al. 2000), turbot (*Scophthalmus maximus*) (Imsland and Jonassen 2001), bay anchovy (*Anchoa mitchilli*) (Lapolla 2001), American shad (*Alosa sapidissima*) (Conover 1990), mummichog (*Fundulus heteroclitus*) (Schultz et al. 1996), and lake sturgeon (*Acipenser fulvescens*) (Power and McKinley 1997). In fact, CnGV in growth is so general that it has also been confirmed in insects (Gotthard et al. 1994; James and Partridge 1995; Arnett and Gotelli 1999), molluscs (Palmer 1994; Parsons 1997; Dittman et al. 1998), amphibians (Laugen et al. 2003), and reptiles (Ferguson and Talent 1993; Niewiarowski and Roosenberg 1993). Such findings demonstrate that adaptive genetic variation in physiological traits that underlay the production capacity of populations is widespread. Coupled with the knowledge from fish breeders that growth rate is also genetically variable within extant populations of many fishes, there appears to be little doubt that the production characteristics of wild populations are capable of evolving.

It is obvious that our empirical simulation of the evolutionary response to harvest lacks realism in many ways. First is the extremely high and accurate size selection differentials that we imposed. Very few fisheries, if any, extract 90% of the population per year and do so with the size-selective accuracy that we enforced. Size-biased harvest in the wild will not exert selection on growth rate as directly as in our experiment and countervailing selection for increased growth may exist in nature, both of which would tend to slow the adaptive response. Second, *Menidia* populations consist of a single age-class that breed in synchrony with environmental cues and hence have non-overlapping generations. Such characteristics in other species would likely complicate the response to selection. For example, in stocks with variation in age at maturity, fishing mortality also tends to select for earlier size and age at maturity (Rijnsdorp 1993; Rochet 1998; Grift et al. 2003) and these traits likely display some level of either positive or negative coheritability with growth rate (see Munch et al. 2005). Hence, the combined effect of harvest selection on both growth rate and size and age at maturity cannot be deduced without knowing both the selection gradient imposed by the fishery and the genetic covariance of the traits in question. Information on these characteristics is not available for most fisheries. Third, we eliminated density dependence by standardizing recruitment each generation. However, had we allowed recruitment to proceed unchecked, the differences in yield among treatments would have been even greater owing to dramatic differences in reproductive potential that emerged among the harvested stocks. The important lesson from *M. menidia* is that evolutionary responses to natural and (or) anthropogenic size-selective mortality exist in nature, are dynamic properties of harvested populations, and hence must be better understood if natural genetic variability for life history traits and the production capacity of populations are to be conserved. Unfortunately, when it comes to predicting evolutionary responses in any particular fishery, the devil is in the stock-specific details of life history strategy, harvest selection gradients, and genetic variances and covariances. Detailed studies of model species could lead the way. We give two examples below.

First, data from model species can provide initial parameterization for population genetic models designed to probe evolutionary responses to harvest mortality. A prime example is the need to account for evolution of the variance–covariance matrix of correlated traits. As our *Menidia* experiments demonstrate, life histories represent a suite of correlated characters that respond in concert to various selective forces. Most studies of evolutionary response to harvest at best consider either growth rate or age at maturity, but in reality, these two traits likely have a genetic covariance that must be known to predict future changes. Such experiments will likely be possible only for a few species that will have to serve as models for others. Second, model species that can be easily cross-bred and reared in the laboratory are needed by molecular biologists to identify the actual genes that control life history. Eventually, molecular tools will allow us to track changes directly in wild populations at the gene level. In anticipation of such developments, depositories providing for routine preservation and storage of tissue samples from harvested populations should be instituted.

In the future, such depositories will likely become as valuable to the study of evolutionary dynamics as catch-per-unit-effort has been to the study of population dynamics.

Conclusions

Despite the inherent difficulties, it is imperative that the evolutionary responses to harvest mortality begin to be addressed. Careful genetic analyses of rapid life history changes following introduction to novel environments are well established in several species (Reznick et al. 1997; Hendry et al. 2000; Quinn et al. 2001) and there is compelling new evidence of long-term changes in size at age (Sinclair et al. 2002; Haugen and Vollestad 2001) or age and size at maturity (Rijnsdorp 1993; Rochet 1998; Grift et al. 2003) in response to harvest in a variety of species. If the above still leaves doubt, consider also that in terrestrial systems, rigorous proof of rapid evolutionary change in response to size-selective hunting now confronts wildlife managers (Coltman et al. 2003). Unfortunately, when changes in response to harvest are genetic, they may be slow to reverse even when fishing stops because cessation of harvest mortality does not automatically ensure that natural agents of selection acting alone will exert sufficient pressure in the reverse direction. For example, Sinclair et al. (2002) showed that declines in size at age of Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) during an intense period of fishing had not reversed in 10 years following a moratorium on harvest. The potential for near irreversibility of directional selection on body size and related traits underscores the need for precautionary approaches.

Fisheries scientists and managers may view dimly the existence of dynamic adaptive variation as just one more complication heaped upon an uncertain science. There are, however, several positive aspects. Knowledge of CnGV in growth, for example, can be used to help aquaculturists find genotypes in the wild with the fastest growth or other beneficial traits, and use of natural genetic variation avoids public disfavor with genetically engineered products. For example, Fontes (1998) showed that striped bass from Nova Scotia and New Brunswick grow much faster under intensive aquaculture conditions than do those from lower latitude stocks. Also, it is possible that harvest regimes might be developed for some wild fisheries that would select for faster rather than slower growth. Freshwater lakes offer an opportunity to test these ideas with replication in the field by using different harvest regimes, such as slot length versus minimum size rules, in multiple systems over several generations followed by common garden experiments (e.g., see an excellent example in Haugen and Vollestad 2001). Finally, the fact that wild populations are capable of rapid genetic adaptation is good news if persistence in the face of environmental change is the ultimate goal.

Empirical models like *M. menidia* play an important role in advancing our fundamental knowledge of fisheries science. Other examples of model species that have provided valuable insights and were studied despite minimal commercial value include bay anchovy and guppy (*Poecilia reticulata*). The broader disciplines of ecology and evolution have a long and successful history of using model species for advancing general knowledge (e.g., *Drosophila*,

Tribolium, *Escherichia coli*, and *Arabidopsis*) and other biological disciplines focus almost all of their attention on a few model species (e.g., the zebrafish model in developmental biology). In fisheries science, we focus most of our attention on the species of greatest economic importance and, of course, this is necessary if we are to develop management plans for them. But all too often, these are the most difficult species to study empirically and hence, new fundamental discoveries come slowly. Species like *M. menidia* where all life stages are extremely easy to sample and study in the field, that have very simple life cycles and behavior, and that can be easily cultured in large captive populations over multiple generations in <1 year offer enormous advantages over most economically important species. Consider that both TSD and CnGV in *M. menidia* were discovered not from a priori theoretical predictions or from thoughtful foresight of the investigators but from incidental observations that were a by-product of studies designed for other purposes. It is the ease with which rigorous comparative field and laboratory observations could be conducted that enabled the findings described above. We argue that greater use of a model species approach will lead to future unforeseen discoveries that will increase our understanding of fish biology and fisheries science.

Acknowledgements

References

Arnett, A.E., and Gotelli, N.J. 1999. Geographic variation in life-history traits of the ant-lion, *Myrmeleon immaculatus*: evolutionary implications of Bergmann's rule. Evolution, **53**: 1180–1188.

Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. J. Fish Biol. **41**(Suppl. B): 137–160.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture, Fisheries and Food, London, UK.

Billerbeck, J.M., Schultz, E.T., and Conover, D.O. 2000. Adaptive variation in energy acquisition and allocation among latitudinal populations of the Atlantic silverside. Oecologia, **122**: 210–219.

Billerbeck, J.M., Lankford, T.E., and Conover, D.O. 2001. Evolution of intrinsic growth and energy acquisition rates: I. Tradeoffs with swimming performance in *Menidia menidia*. Evolution, **55**: 1863–1872.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C., and Festa-Bianchet, M. 2003. Undesirable evolutionary consequences of trophy hunting. Nature (Lond.), **426**: 655–658.

Conover, D.O. 1984. Adaptive significance of temperature-dependent sex determination in a fish. Am. Nat. **123**: 297–313.

Conover, D.O. 1985. Field and laboratory assessment of patterns in fecundity of a multiple spawning fish: the Atlantic silverside, *Menidia menidia*. Fish. Bull. **83**: 331–341.

Conover, D.O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. Trans. Am. Fish. Soc. **119**: 416–430.

Conover, D.O. 1998. Local adaptation in marine fishes: evidence and implications for stock enhancement. Bull. Mar. Sci. **62**: 305–311.

Conover, D.O. 2004. Temperature-dependent sex determination in fishes. *In* Temperature-dependent sex determination. *Edited by* N. Valenzuela and V. Lance. Smithsonian Institution Press, Washington, D.C. pp. 11–20.

Conover, D.O., and Heins, S.W. 1987. Adaptive variation in environmental and genetic sex determination in a fish. Nature (Lond.), **326**: 496–498.

Conover, D.O., and Kynard, B.E. 1981. Environmental sex determination: interaction of temperature and genotype in a fish. Science (Wash., D.C.), **213**: 577–579.

Conover, D.O., and Kynard, B.E. 1984. Field and laboratory observations of spawning periodicity and behavior of a northern population of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). Environ. Biol. Fishes, **11**: 161–171.

Conover, D.O., and Munch, S.B. 2002. Sustaining fisheries yields over evolutionary time scales. Science (Wash., D.C.), **297**: 94–96.

Conover, D.O., and Murawski, S.A. 1982. Offshore winter migration of the Atlantic silverside *Menidia menidia*. Fish. Bull. **80**: 145–149.

Conover, D.O., and Present, T.M.C. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia, **83**: 316–324.

Conover, D.O., and Ross, M.R. 1982. Patterns in seasonal abundance, growth, and biomass of the Atlantic silverside, *Menidia menidia*, in a New England estuary. Estuaries, **5**: 275–286.

Conover, D.O., and Schultz, E.T. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends Ecol. Evol. **10**: 248–252.

Conover, D.O., and Van Voorhees, D.A. 1990. Evolution of a balanced sex ratio by frequency-dependent selection in a fish. Science (Wash., D.C.), **250**: 1556–1558.

Conover, D.O., Brown, J.J., and Ehtisham, A. 1997. Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. Can. J. Fish. Aquat. Sci. **54**: 2401–2409.

Devlin, R.H., and Nagahama, Y. 2002. Sex determination and sex differentiation in fish: an overview of genetic, physiological, and environmental influences. Aquaculture, **208**: 191–364.

Dittman, D.E., Ford, S.E., and Haskin, H.H. 1998. Growth patterns in oysters, *Crassostrea virginica*, from different estuaries. Mar. Biol. **132**: 461–469.

Ferguson, G.W., and Talent, L.G. 1993. Life history traits of the lizard *Sceloporus undulates* from two populations raised in a common laboratory environment. Oecologia, **93**: 88–94.

Fontes, D.S. 1998. Countergradient latitudinal variation in somatic growth rate of striped bass (*Morone saxatilis*): physiological mechanisms and implications. M.S. thesis, Stony Brook University, Stony Brook, N.Y.

Gotthard, K., Nylin, S., and Wiklund, C. 1994. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. Oecologia, **99**: 281–289.

Grift, R.E., Rijnsdorp, A.D., Barot, S., Heino, M., and Dieckmann, U. 2003. Fisheries-induced trends in reaction norms for maturation in North Sea plaice. Mar. Ecol. Prog. Ser. **257**: 247–257.

Haugen, T.O., and Vollestad, L.A. 2001. A century of life-history evolution in grayling. Genetica, **112**: 475–491.

Hendry, A.P., Wenburg, J.K., Bentzen, P., Volk, E.C., and Quinn, T.P. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science (Wash., D.C.), **290**: 516–518.

Hurst, T.P., and Conover, D.O. 1998. Winter mortality of young-of-the-year Hudson River striped bass (*Morone saxatilis*): size-dependent patterns and effects on recruitment. Can. J. Fish. Aquat. Sci. **55**: 1122–1130.

Imsland, A.K., and Jonassen, T.M. 2001. Regulation of growth in turbot (*Scophthalmus maximus* Rafinesque) and Atlantic halibut (*Hippoglossus hippoglossus* L.): aspects of environment × genotype interactions. Rev. Fish Biol. Fish. **11**: 71–90.

James, A.C., and Partridge, L. 1995. Thermal evolution of the rate of larval development in *Drosophila melanogaster* in laboratory and field populations. J. Evol. Biol. **8**: 315–330.

Jessop, B.M. 1983. Aspects of the life history of the Atlantic silverside (*Menidia menidia*) of the Annapolis River, Nova Scotia. Can. Manuscr. Rep. Fish. Aquat. Sci. No. 1694.

Jonassen, T.M., Imsland, A.K., Fitzgerald, R., Bonga, S.W., Ham, E.V., Naevdal, G., Stefansson, M.O., and Stefansson, S.O. 2000. Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. J. Fish Biol. **56**: 279–294.

Klahre, L. 1998. Countergradient variation in egg production rate of the Atlantic silverside, *Menidia menidia*. M.S. thesis, Stony Brook University, Stony Brook, N.Y.

Lankford, T.E., Billerbeck, J.M., and Conover, D.O. 2001. Evolution of intrinsic growth and energy acquisition rates: II. Trade-offs with vulnerability to predation in *Menidia menidia*. Evolution, **55**: 1873–1881.

Lapolla, A.E. 2001. Bay anchovy *Anchoa mitchilli* in Narragansett Bay, Rhode Island. I. Population structure, growth and mortality. Mar. Ecol. Prog. Ser. **217**: 93–102.

Laugen, A.T., Laurila, A., Rasanen, K., and Merila, J. 2003. Latitudinal countergradient variation in the common frog (*Rana temporaria*) development rates — evidence for local adaptation. J. Evol. Biol. **16**: 996–1005.

Middaugh, D.P., Domey, R.G., and Scott, G.I. 1984. Reproductive rhythmicity of the Atlantic silverside. Trans. Am. Fish. Soc. **113**: 472–478.

Munch, S.B., and Conover, D.O. 2002. Accounting for local physiological adaptation in bioenergetic models: testing hypotheses for growth rate evolution by virtual transplant experiments. Can. J. Fish. Aquat. Sci. **59**: 393–403.

Munch, S.B., and Conover, D.O. 2004. Nonlinear growth cost in *Menidia menidia*: theory and empirical evidence. Evolution, **58**: 661–664.

Munch, S.B., Mangel, M., and Conover, D.O. 2003. Quantifying natural selection on body size from field data with an application to winter mortality in *Menidia menidia*. Ecology, **84**: 2168–2177.

Munch, S.B., Walsh, M.R., and Conover, D.O. 2005. Harvest selection, genetic correlations, and evolutionary changes in recruitment: one less thing to worry about? Can. J. Fish. Aquat. Sci. **62**: 802–810.

Niewiarowski, P.H., and Roosenberg, W. 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulates*. Ecology, **74**: 1992–2002.

Palmer, A.R. 1994. Temperature-sensitivity, rate of development, and time to maturity: geographic variation in laboratory-reared *Nuculla* and a cross-phyletic overview. *In* Reproduction and development of marine invertebrates. *Edited by* W.H. Wilson, S.A. Stricker, and G.L. Shinn. Johns Hopkins University Press, Baltimore, Md. pp. 177–194.

Parsons, K.E. 1997. Contrasting patterns of heritable geographic variations in shell morphology and growth potential in the marine gastropod *Bembicium vittatum*: evidence from field experiments. Evolution, **51**: 784–796.

Power, M., and McKinley, R.S. 1997. Latitudinal variation in lake sturgeon size as related to the thermal opportunity for growth. Trans. Am. Fish. Soc. **126**: 549–558.

Present, T.M.C., and Conover, D.O. 1992. Physiological basis of latitudinal growth differences in *Menidia menidia*: variation in consumption or efficiency? Funct. Ecol. **6**: 23–31.

Quinn, T.P., Kinnison, M.T., and Unwin, M.J. 2001. Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. Genetica, **112**: 493–513.

Reznick, D.N., Shaw, F.H., Rodd, F.H., and Shaw, R.G. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science (Wash., D.C.), **275**: 1934–1937.

Rijnsdorp, A.D. 1993. Fisheries as a large-scale experiment on life-history evolution — disentangling phenotypic and genetic-effects in changes in maturation and reproduction of North-Sea plaice, *Pleuronectes platessa*. Oecologia, **96**: 391–401.

Rochet, M.J. 1998. Short-term effects of fishing on life history traits of fishes. ICES J. Mar. Sci. **55**: 371–391.

Roff, D.A. 2002. Life history evolution. Sinauer Associates, Sunderlund, Mass.

Schultz, E.T., and Conover, D.O. 1997. Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia menidia*). Oecologia, **109**: 516–529.

Schultz, E.T., Reynolds, K.E., and Conover, D.O. 1996. Countergradient variation in growth among newly-hatched *Fundulus heteroclitus*: geographic differences revealed by common-environment experiments. Funct. Ecol. **10**: 366–374.

Schultz, E.T., Conover, D.O., and Ehtisham, A. 1998. The dead of winter: size-dependent variation and genetic differences in seasonal mortality among Atlantic silversides (Atherinidae: *Menidia menidia*) from different latitudes. Can. J. Fish. Aquat. Sci. **55**: 1149–1157.

Sinclair, A.F., Swain, D.P., and Hanson, J.M. 2002. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. Can. J. Fish. Aquat. Sci. **59**: 361–371.

Walsh, M.R. 2003. Evolution in response to size-selective mortality: changes in correlated characters among captive populations of the Atlantic silverside (*Menidia menidia*). M.S. thesis, Stony Brook University, Stony Brook, N.Y.