

ORIGINAL ARTICLE

Habitat-mediated size selection in endangered Atlantic salmon fry: selectional restoration assessment

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Abstract

Preservation of adaptive variation is a top priority of many species restoration programs, but most restoration activities are conducted without direct knowledge of selection that might foster or impair adaptation and restoration goals. In this study, we quantified geographic variation in selection on fry size of endangered Atlantic salmon (*Salmo salar*) during the 6-week period immediately following stocking in the wild. We also used a model selection approach to assess whether habitat variables influence patterns of such selection. We found evidence for significant size-selection in five out of six selection trials. Interestingly, the strength and pattern of selection varied extensively among sites, and model selection suggested that this variation in phenotypic selection was related to geographic variation in the presence of large woody debris and the slope of the stream gradient. The strong selection differentials we observed should be a concern for endangered salmon restoration, whether they reflect natural processes and an opportunity to maintain adaptation, or an indicator of the potentially deleterious phenotypic consequences of hatchery practices.

Introduction

Size at age is considered a critical adaptive trait for most organisms. For many species, larger size at age is thought to increase predator escape ability, environmental tolerances, and competitive ability, promote earlier maturation, and contribute to greater fecundity (reviewed in Sogard 1997). However, larger size at age is not always beneficial (Sogard 1997; Hendry et al. 2003). Larger individuals may require different resources than smaller individuals, be more conspicuous to some predators due to their size or behavior, or may not have access to some size-limited refuges (Miller et al. 1988; Litvak and Leggett 1992). Energetically, larger size may often necessitate greater time and risk associated with foraging (Metcalf et al. 1995), and somatic investment may reduce investment in other physiological allocations, such as reproduction (Rowe et al. 1991). Optimal size at age presumably varies in space and time depending on a number of costs and benefits specific to local environmental conditions. Understanding how selection for size at age varies geographically and with habitat features is important in understanding the origins and maintenance of size and

traits linked to size. Perhaps nowhere is such adaptive insight more practically significant than for endangered or threatened species. However, measures of natural selection have yet to be widely incorporated in the designation or management of threatened species. Here, we show that such a 'selectional' assessment is both feasible and informative.

Atlantic salmon (*Salmo salar*) undergo a series of early life-history transitions: from embryo (egg) to yolk-sac larva (alevin), that develop within the gravel; to free swimming juveniles (fry) that emerge from the gravel to establish and defend feeding territories (Gustafson-Greenwood and Moring 1990). The days following emergence are considered a critical period for survival, with larger size generally thought to be beneficial for territorial dominance, swimming ability and predator avoidance (Metcalf et al. 1989; Einum and Fleming 2000). However, prior work (e.g., Good et al. 2001) has found that size-selective mortality can vary temporally with abiotic conditions. Thus, salmon fry do not always follow the bigger-is-better pattern. Even still, size-selective mortality theoretically contributes to lifetime mortality rates, and may even influence the size-dependent life history patterns expressed in populations,

such as age at migration to sea or reproduction (Thorpe et al. 1998; Aubin-Horth et al. 2005).

Many populations of anadromous Atlantic salmon have undergone precipitous declines in abundance over the last century (USASAC 2008). One widely-employed restoration approach for salmon entails the release of hatchery-reared fry, bypassing mortality during the egg and alevin stages. Fry are stocked in the spring, when they are exposed to high flows, low temperatures and high predation risk (Egglisshaw and Shackley 1980; Letcher and Terrick 2001). Mortality of fry is thus generally high, decimating numbers by as much as 60% within the first two weeks poststocking (Henderson and Letcher 2003). Traditionally, hatcheries have often sought to produce fry that are relatively large and advanced compared to natural populations to improve perceived odds of survival following release. This has been variously accomplished by thermally accelerating fry development, feeding fry prior to release, or preferential use of larger fry for stocking. However, despite the very large numbers of fry that are released for restoration (i.e., hundreds of thousands to millions in many programs), fry stocking has met with mixed success as a restoration tool (Ritter 1997).

Nonetheless, stocking fry is often advocated over stocking strategies using later life stages, in large part because fry are considerably less expensive to rear and the minimal time in the hatchery is thought to reduce opportunities for inadvertent domestication selection (Stolte 1983; Weber and Fausch 2003). Fry stocking is also commonly presumed to offer greater opportunities for exposure to natural patterns of selection and retention of local adaptation (Youngson and Verspoor 1998; Aprahamian et al. 2003). However, few hatchery programs conduct their rearing and stocking programs with direct knowledge of the patterns of natural selection that presumably contribute to fry abundance and size structure in the wild. We suggest this can contribute to a 'one size fits all' strategy that ignores potential variation in selection across the geographic range being stocked. Such a strategy may fail to optimize, or even imperil, local adaptation and recovery of threatened salmon stocks.

In this study, we sought to characterize geographic variation in size selection on stocked Atlantic salmon fry, and to relate that selection to local habitat features that are commonly assessed as part of salmon restoration planning. To examine selective mortality we used otolith-back-calculation methods similar to Meekan et al. (1998) to evaluate mortality based on size of individuals at time of stocking. Other investigations have used similar approaches to determine size-selective mortality of wild fry under different contexts and life stages (interannual selection: Good et al. 2001; winter mortality: Johnston et al. 2005; links to precocious maturation: Aubin-Horth

and Dodson 2004). We assessed size-selective mortality over the first 6-weeks following stocking at six different locations, spanning five river-specific populations within the federally endangered Gulf of Maine Distinct Population Segment (GOMDPS). In so doing, we provide an initial 'selectional' assessment of the current evolutionary status of this conservation unit.

Methods

Study system

In 2000, the Gulf of Maine Distinct Population Segment (GOMDPS) of Atlantic salmon was listed under the US Endangered Species Act (ESA) due to dangerously reduced spawning runs and low juvenile densities [National Research Council (NRC) 2004]. The listing included populations in eight Maine rivers (Machias, Narraguagus, Sheepscot, East Machias, Dennys, Pleasant, Ducktrap, and Cove Brook). Six of these populations are maintained through supplemental breeding at the United States Federal Fish and Wildlife Service's Craig Brook National Fish Hatchery (CBNFH) in East Orland, ME, where river-specific parents are used to produce fry that are in turn stocked back into the rivers. Hatchery rearing to the fry stage largely bypasses high embryo and larval mortality that occurs in redds over winter, and stocking fry seeks to increase the number available to enter the critical period of transition to exogenous feeding.

Stocking and sampling

In 2004, fry were stocked into six streams (Fig. 1) as part of normal restoration operations by staff from the University of Maine, Maine Department of Marine Resources, and CBNFH. The fry used in these stocking trials were from five of the endangered river-specific broodstock sources maintained at CBNFH. Fry were distributed from canoes or on foot at normal stocking densities of 50–100 fry per 100 m² of habitat. The six sites in 2nd and 3rd order streams were distributed among five river systems: mainstem of the Dennys River (DEN), mainstem of the East Machias (EMA), Mopang Stream in the Machias River (MOP), Shorey Brook in the Narraguagus River (SHO), a mainstem site (SMA) in the Sheepscott River, and a site in the West Branch of the Sheepscott (SWB). On the day of stocking, we collected a sample of at least 78 fry to assess the size-structure of the population at stocking and to develop size-otolith relationships. Subsequently, samples of roughly 50 fry were collected 6-weeks (42 days) after stocking using electrofishing (400–500 V unpulsed DC; Smith-Root Backpack electroshocker) in a random pattern throughout each study site

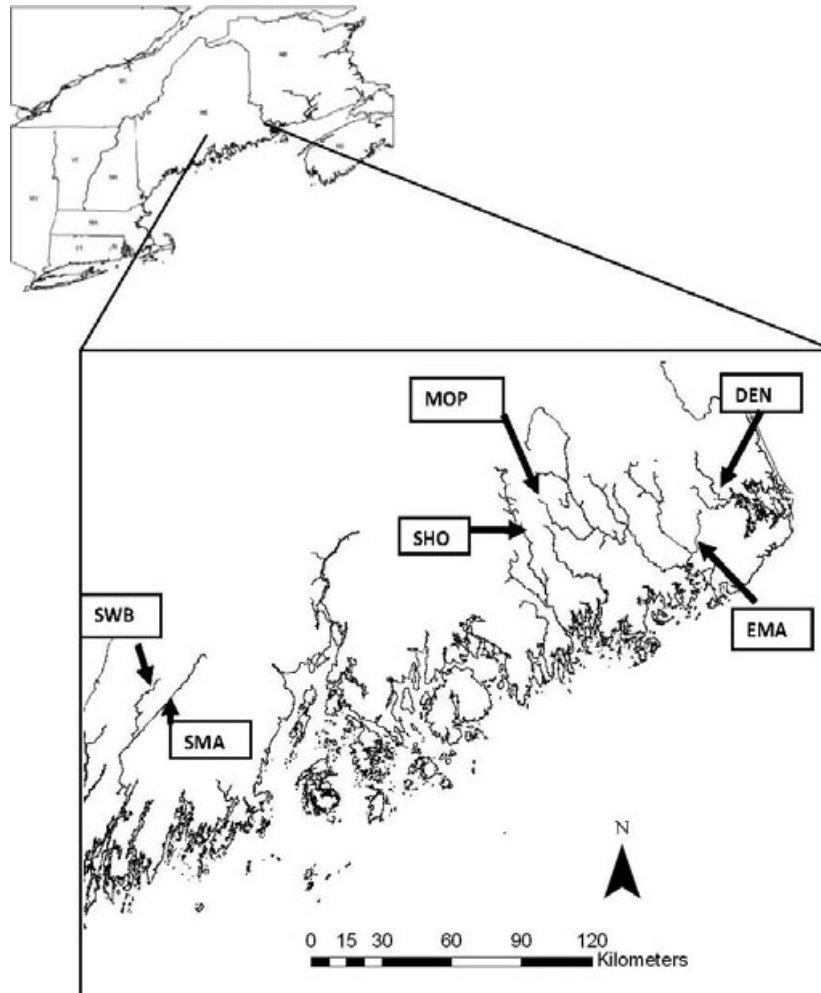


Figure 1 Map of the State Maine and surrounding area, with circles representing the streams stocked with Atlantic salmon (*Salmo salar*) fry and later resampled for estimates of size-selective mortality. Dennys River (DEN), East Machias River (EMA), Mopang Stream (MOP), Shorey Brook (SHO), Sheepscot River mainstem (SMA) and West Branch of Sheepscot River (SWB).

(sample sizes were restricted by Federal ESA permitting). In order to remove any microhabitat effects and any differential movement of individuals, we sampled over a large area (hundreds of meters) and in both high quality and low quality areas. We used small-meshed dipnets to avoid size-biased captures. All fry were immediately euthanized in water with buffered MS-222 at concentrations of 1000 mg/L and then transferred to 95% ETOH as a fixative.

Otolith preparation

Calipers were used to measure standard length after alcohol fixation. Right and left sagittal otoliths were dissected from all fry using a dissecting microscope with a polarized light. Otoliths were then cleaned and placed in

epoxy on a microscope slide and sanded with lapping film to the level of the otolith core. Otolith preparations were viewed using a compound microscope, linked by a high-resolution camera to a video monitor and computer at magnifications of 250 and 400 \times . Otolith total radius length and radius length at stocking (for recaptured fry) were measured along a consistent axis, defined as a line starting in the central nucleus and forming a 45-degree angle with the posterior axis in the ventral region (Johnston et al. 2005). To ensure accuracy, otolith measures were only recorded when both sagittal otoliths were available and the reader was able to determine a clear stocking mark on each. Stocking checks were verified on a subsample of ten otoliths from different individuals via counting daily rings from stocking check to edge.

Size analysis

The relationship between total length at time of stocking and otolith radius was determined for each river-specific broodstock source using the otoliths of fry collected at stocking and ANCOVA (dependent = fish length; independent = brood; covariate = otolith radius). The total lengths at stocking of subsequently resampled individuals were estimated by back-calculation using these ANCOVA relationships and the biological intercept technique of Campana and Jones (1992). Meekan et al. (1998) have validated assumptions of the back calculation technique for Atlantic salmon young-of-the-year.

T-tests comparing the mean lengths of prestocking and recaptured fish were used to assess the potential significance of directional selection (Meekan et al. 1998; Good et al. 2001). Standardized linear selection differentials (*i*) were estimated for each stocking trial as the difference between the mean size at stocking of all released fish and the mean size at stocking of the recaptured sample, divided by the standard deviation of fry size at stocking. This standardized selection measure allowed us to compare the strengths of selection in the present study with selection estimates from the broader literature (i.e., Kingsolver et al. 2001).

Habitat characteristics

Habitat characteristics of each stocking site were obtained from the Maine Department of Marine Resources (MDMR) Atlantic Salmon Habitat Database (unpublished data). This database is used by MDMR to rate salmon habitat as suitable or not suitable for salmon stocking and restoration purposes. Habitat sampling is similar to methods in Platts et al. (1983). Briefly, field surveys were combined with GIS layers to classify stream reaches (riffle-runs, pools, etc.), bottom structure (i.e., substrate), stream slope, woody debris availability and width. All stocking occurred in sites classified in this database as riffle-run habitat with suitable bottom structure. However, our sites did differ in terms of stream slope (derived from section gradient data and logged for normality), average stream width, and a binary indicator of 'presence or absence' of large-woody-debris (LWD). Average stream slope for a given study site was estimated using only the slopes from component sections with appropriate habitat (i.e. pool and very high gradient riffles were not included).

We performed a model selection analysis to determine whether and how the above habitat variables might be related to observed variation in selection among study sites. Corrected Akaike's information criterion (AIC_c) was used to select the best model relating habitat features to

selection differentials without over-fitting the number of variables. Parameter estimates and statistical significance of factors within the best model(s) were evaluated using standard least-squares regression.

Results

Fry sampling

Adequate numbers of fry were recaptured within 1 or 2 days of sampling at each site (DEN sample date July 1; MOP recapture date July 1 and July 2; SWB recapture date June 22; EMA recapture date July 2; SHO recapture date June 16 and SMA recapture date June 22; Table 1). Although our goal was to sample 50 individuals per site, pursuant to prudent sampling of an endangered species, the effective sample size was often smaller (between 24 and 35 individuals) because otoliths were not always successfully extracted from some fish, some otoliths were lost or damaged during processing (10–20%), and stocking 'checks' were not clearly identifiable on both otoliths from a small number of individuals. Counts of daily growth rings between the nominal stocking check and otolith margin for a subset of Shorey brook fish ($n = 10$) confirmed that our nominal stocking checks were indeed associated with the actual time of stocking and thus suitable to provide an estimate of otolith size and fish size at stocking.

Otolith and somatic growth

Otolith radius and standard length of salmon at stocking were related at all sites ($F = 189.8169$, $P < 0.0001$). However, regressions for different population sources were not parallel ($F = 15.2127$, $P < 0.0001$). Homogeneous population subsets were identified using Tukey's multiple comparisons. Ultimately, individual length and otolith

Table 1. Sample sizes of fry collected at stocking, mean length at stocking, sample size of fry used for length and otolith relationship development, and number of resampled fry used for back calculations.

Site	# individuals sampled at stocking	Mean length at stocking (mm)	# used for length-otolith relationship	# used for back calculation
DEN ¹	78	26.74	23	35
EMA ²	135	25.44	26	24
MOP ¹	91	25.84	33	26
SWB ¹	291	26.20	29	35
SHO ²	108	27.78	45	29
SMA ²	79	25.93	29	35

^{1,2}Homogeneous regression subsets for otolith size—fish size back calculations.

relationships were pooled into two homogenous population subset regressions for back calculation purposes ($n = 85$, $P < 0.0001$, $r^2 = 0.56$ for DEN, MOP and SWB and $n = 100$, $P < 0.0001$, $r^2 = 0.68$ for EMA, SHO and SMA; Fig. 2). Back-calculated distributions of fry body length at stocking for resampled fish significantly differed from the full population length distributions at stocking in five of the six selection trials (DEN t -test: $t_{1,112}$ $P = 0.030$; EMA t -test: $t_{1,158}$ $P = 0.004$; MOP t -test: 2000, $t_{1,116}$ $P = 0.0005$; SWB t -test: $t_{1,325}$ $P = 0.0001$; SHO t -test: $t_{1,163}$ $P = 0.219$ and SMA t -test: $t_{1,113}$ $P < 0.0001$ (Fig. 3, Table 2). The standardized linear selection differentials estimated for these 6-week bouts ranged from absolute values of 0.25–0.89, which compares with the 70th to 96th percentiles of values from the broader literature, as summarized by Kingsolver et al. (2001).

Habitat modeling

Models based on either LWD or stream slope were equally likely without over-parameterization ($\Delta AIC_C \leq 2.3$) and explained between 56% and 70% of the variation in observed selection differentials. Models combining the LWD and stream slope, or including stream width, were much less likely to be predictive, albeit a model including

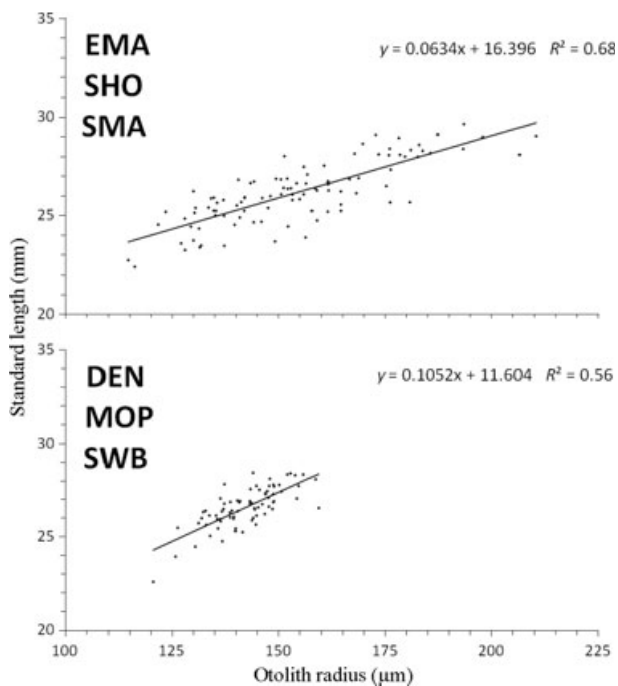


Figure 2 Relationships between standard length of Atlantic salmon (*Salmo salar*) fry and otolith radius for six streams in Maine, USA. Streams are grouped into two homogeneous subsets ($P < 0.001$ for both relationships).

LWD and stream width had the largest model r^2 (Table 3). Overall, selection favored larger fish in sites with more LWD ($P = 0.038$; Fig. 4). Selection tended to favor smaller fish in sites with lower overall slope, albeit the pattern was at best marginally significant ($P = 0.086$; Fig. 5).

Discussion

Strong selection on fry body size occurred at multiple stocking sites within the geographic range of the Gulf of Maine Distinct Population Segment. Interestingly, the strength and pattern of size selection was highly variable among rivers. In this respect, our observations coincide with general theory, but again disagree with the common salmon management perception that larger size at stocking is generally advantageous to the survival of young fish (West and Larkin 1987; Elliott 1990). Larger size was selected against in several of our selection trials. We also found novel evidence that geographic variation in natural selection on hatchery fry is related in part to local habitat attributes. We now turn to a discussion of our findings with respect to other studies of selection, particularly in salmonids, the role of local conditions in mediating the strength and pattern of selection, and implications of incorporating selection analyses in the management of threatened species.

Spatio-temporal variation in size-selection

Juvenile salmonids live in spatially and temporally variable stream environments. It is logical that such environments foster spatio-temporal variation in selection. Good et al. (2001) and Carlson et al. (2004) both found that selection on wild juvenile salmon can be variable in both strength and direction. Carlson et al. (2004) studied juvenile salmon at later life stages (parr in their first winter after hatch), but Good et al. (2001) considered fry over their first summer of life; which overlaps with the period of our study. However, Good et al. (2001) considered selection among sites within a single river system and variation in selection between years. The greatest variation in selection observed by Good et al. (2001) corresponded to differences between years, with much less evidence of spatial heterogeneity in selection among sites within their drainage. In contrast, we focused on spatial variation in selection across the geographic range of five river systems, each of which is thought to support a locally adapted population (Obedzinski and Letcher 2004; Sheehan et al. 2005; N. Wilke unpublished data). It is perhaps thus fitting that we found much more evidence of spatial heterogeneity in selection in the present study, providing support for a mechanistic basis for adaptive divergence

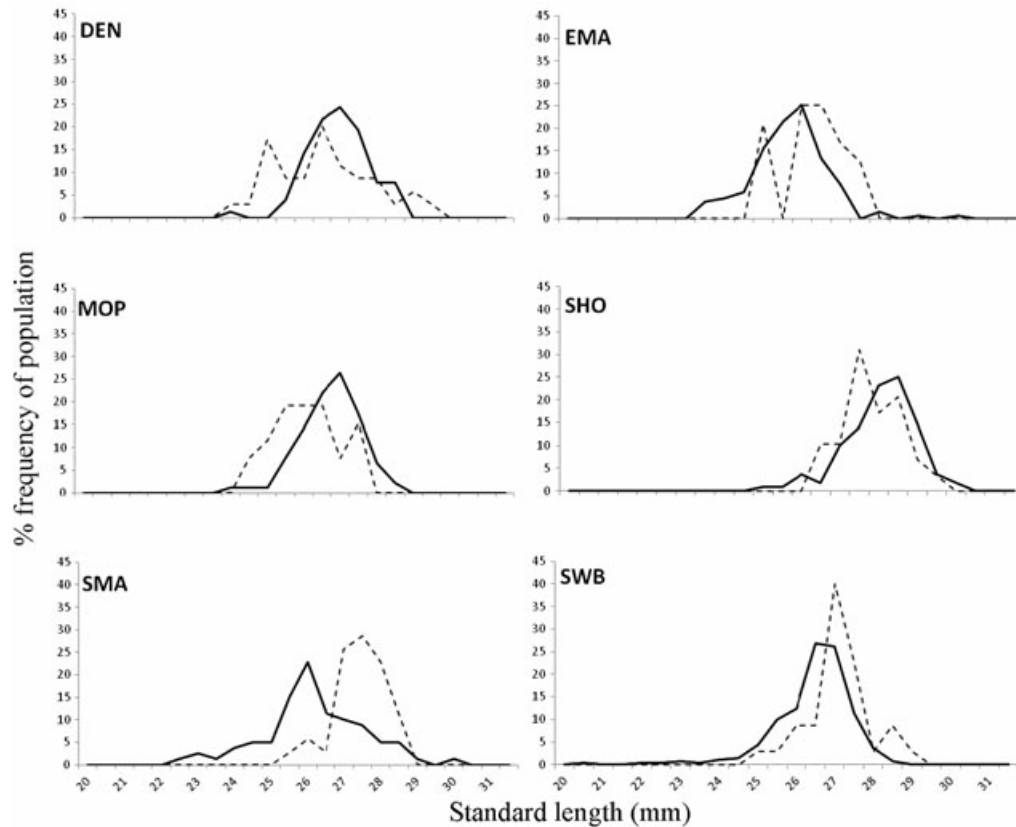


Figure 3 Comparison of the standard length distributions for Atlantic salmon (*Salmo salar*) fry at stocking (solid lines) and the back-calculated standard lengths of fry resampled from streams 6 weeks later (dashed lines).

across this range. That said, it is worth noting that the two trials we conducted within a single river system (the Sheepscott) showed similar patterns of selection, consistent with the relative intradrainage homogeneity of Good et al. (2001).

In combination, these observations of relative homogeneity of selection within river systems, but heterogeneity

among systems, could reflect a tendency for habitat attributes to differ more among systems or for genetic divergence to influence how populations respond to environmental conditions. We could not test the latter effect because it is not permissible under current endangered salmon management practices to release fish from multiple river-specific sources at a given site within the protected range of the species. However, we were able to assess the potential for specific attributes of habitat heterogeneity to influence patterns of selection across the GOMDPS.

Even given the relatively limited power expected with only six selection trials (data points) it is noteworthy that we found model support for effects of large woody debris and stream gradient (as measured by slope) on the strength and pattern of selection. Our study is thus unique in linking variation in selection on juvenile salmon to variation in their local habitat attributes. Although other studies have documented selection in juvenile salmon, or have shown that habitat features like large woody debris may promote survival or growth (Roni and Quinn 2001; Giannico and Hinch 2003), we believe this is the first study to provide evidence that local

Table 2. Standard body length (mm) at stocking, back-calculated length (mm) at stocking, shift in mean length (mm), standardized selection differential and *P*-value for *T*-test of change in average length of Atlantic salmon (*Salmo salar*) fry.

Site	Measured at stocking	Back-calculated at stocking	Mean shift	Standardized selection differential	<i>P</i> -value
DEN*	26.74 (0.83)	26.28 (1.40)	-0.46	-0.56	0.030
EMA†	25.44 (1.00)	26.07 (0.89)	0.63	0.63	0.004
MOP*	26.50 (0.80)	25.84 (0.93)	-0.66	-0.83	<0.001
SHO†	27.78 (0.92)	27.55 (0.76)	-0.23	-0.25	0.219
SMA†	25.93 (1.39)	27.15 (0.73)	1.22	0.89	<0.001
SWB*	26.20 (1.01)	26.89 (0.82)	0.69	0.68	<0.001

Standard deviations are in parenthesis.

Table 3. Model selection of site attributes on size selection differentials in hatchery released Atlantic salmon (*Salmo salar*) fry.

Model	AIC _c	ΔAIC _c	R ²
LWD	22.9	–	0.70
LOG ₁₀ SLOPE*	25.2	2.3	0.56
WIDTH	30.1	7.2	0.01
LWD + LOG ₁₀ SLOPE	51.1	28.2	0.78
LWD + WIDTH	51.4	28.4	0.88

Akaike’s information criterion corrected for small sample size (AIC_c) and the difference (ΔAIC_c) between the AIC_c value for a particular model and the competing regression model with lowest AIC_c. Variables in italics were individually significant in regression models at *P* < 0.05.

*Marginally significant at *P* = 0.086.

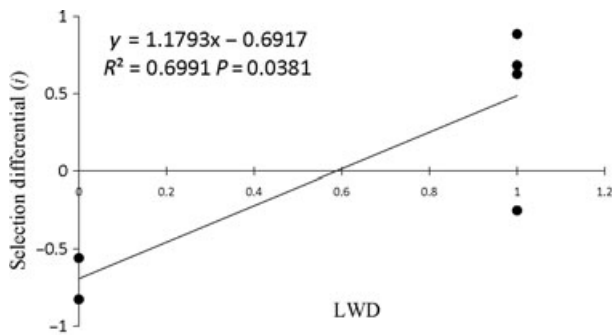


Figure 4 Standardized selection differentials (*i*) relative to presence of large woody debris (LWD) for six streams in Maine, USA.

habitat attributes, such as the presence of woody debris, has implications for patterns of selection that shape juvenile size distributions. In this respect, the current study is akin to studies that have shown how other habitat attributes, like the accessibility by predators (e.g., bears) and water depth, can influence patterns of selection on adult salmon size and morphology (e.g., Quinn and Kinnison 1999; Carlson et al. 2009).

Hypotheses for habitat/selection correlations

We suggest two functional mechanisms for the observed relationship between the presence of woody debris and selection for larger fry size. These hypotheses could be readily tested with future mechanistic studies. First, LWD promotes habitat heterogeneity (reviewed in Schlosser 1991), which may in turn increase the variance in resource availability and territory quality. Greater variation in habitat quality favors intraspecific competition for quality habitats and thus the competitive ability of large fry. Second, LWD may provide improved habitat for fishes that prey on salmon fry, such as brook charr (*Salvelinus fontinalis*; Roghair et al. 2002). The presence

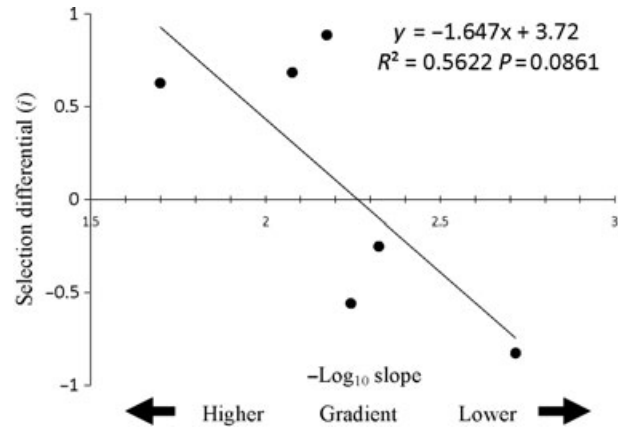


Figure 5 Standardized selection differentials (*i*) relative to $-\log_{10}$ slope of suitable habitat for six streams in Maine, USA.

of such predators may select for the superior predator escape performance of large fry.

Of course, a less mechanistic explanation for the observed relationship is that LWD is coincidentally correlated with some other habitat attribute that is responsible for selection on fry size. For example, LWD may be correlated with steeper stream gradients (or vice versa). That said, LWD showed a stronger correlation with selection on salmon than did stream slope, and we do not have sufficiently detailed data on the landscape and hydrological features of our study sites to directly link deposition of woody debris to flow regime. Regardless, it is important to note that even if LWD and stream slope are spatially correlated, this would not rule out an actual functional role for LWD. When LWD and stream slope are in the same model (Table 3.) it does improve the overall fit of the model ($r^2 = 0.78$), albeit such a model is not the most parsimonious for the data (ΔAIC_c = 28.2).

Although not statistically significant given our limited power, the trend we detected between stream gradient and selection for fish size is intuitive on several grounds. Streams with steeper slopes would have higher velocities and other habitat attributes often linked to flow, such as shorter pool-riffle structure and courser substrate (Allan 1995). These habitat attributes may favor larger fry due to their enhanced swimming capabilities and superior ability to monopolize habitat patches of high quality (Johnsson et al. 1999). Abrupt increases in discharge during spring floods may even wash out small fish with limited swimming ability (Heggenes and Traaen 1988, Ottaway and Clarke 1981). Although fish may quickly grow out of this risk (Jensen and Johnsen 1999), the greatest seasonal period of flooding risk in Maine occurs in early spring and corresponds with the period of fry stocking and wild fry emergence. In contrast, stream sections with flatter gradients tend to support slower flows, longer riffles and

runs and finer substrates (Allan 1995), which may in turn favor smaller fry. However, hypothesized mechanisms favoring smaller fry in such habitats are somewhat more challenging to conceive. Perhaps smaller fry are better suited to the refuges and food resources available in such habitats.

Prior studies of selection on juvenile salmon support the premise that hydrological conditions can influence whether larger or smaller fry are favored by mortality selection. Specifically, Good et al. (2001) concluded that interannual variation in hydroclimate conditions was responsible for balancing selection on fry size across years. However, Good et al. (2001) found that large fry were favored in a drought (i.e., low flow) year, due to their suggested ability to compete for limited territories, whereas small fry were favored in a flood year, purportedly due to their ability to seek out and occupy refuges during high water events. This difference between studies suggests that flow alone may not be sufficient to reconcile spatial and temporal patterns of size selection.

Linking selection and management

In the present study, selection was not only variable but also very strong (range: -0.83 to 0.89). Kingsolver et al. (2001) reported that 87% of published linear selection differentials have absolute values less than 0.50, and 95% are less than 0.75. Hence, the standardized differentials from our trials at MOP and SMA were stronger than 95% of the values summarized by Kingsolver et al. (2001) and the differentials for DEN, SWB and EMA were all greater than 87% of published values. Only the SHO selection estimate was not statistically significant and modest relative to values in the literature. The strong selection we have documented in this study is not just academically interesting; we suggest that it should be of concern to managers involved in endangered salmon restoration.

Maine Atlantic salmon are known to exhibit a high degree of fidelity to their native streams (Spidle et al. 2001) and differences in morphology and life history traits consistent with local adaptation to their source rivers (Sheehan et al. 2005; Obedzinski and Letcher 2004; N. Wilke unpublished data). Preserving river specific adaptations is thus a top priority for the Maine salmon restoration program (NMFS and USFWS 2005). Strong selection suggests that current distributions of fry size at stocking are not precisely matched to current salmon habitat conditions in Maine. We suggest that there are at least three possible explanations for the observed strong (and variable) selection: (i) such selection may be the norm under natural conditions, (ii) it could reflect degraded habitat quality or (iii) it could reflect problems with the current genetic resource.

Strong selection may persist in nature because overall fitness is not maximized by one component of fitness (Schluter et al. 1991), such as early fry survival. Likewise, as suggested by Good et al. (2001) and Carlson et al. (2004), selection may be naturally variable in time, preventing local populations from fully attaining a precise adaptive optimum (albeit this explanation is somewhat at odds with the habitat correlations we detected). If the selection we observed reflects natural patterns that are divergent among river systems, it is imperative that Maine's river-specific salmon stocks be managed as largely separate populations to preserve any associated local adaptations. Moreover, populations may benefit from continued exposure to such selection in order to maintain overall adaptation under the influence of potential competing selection at other life stages.

The possibility that the selection we observed results from less natural causes is much more troubling. Maine's river systems have experienced nearly two centuries of human modifications, including streambed engineering, sedimentation from activities in the surrounding landscape, and removal of woody debris (NRC 2004). Maine's salmon populations may thus face strong selection as their habitat changes around them. The question in this case is whether these salmon can in turn evolve fast enough to keep pace with such change (Gomulkiewicz and Holt 1995; Kinnison and Hairston 2007). Studies of introduced salmon populations suggest juvenile size can evolve in contemporary time (Kinnison et al. 1998; Unwin et al. 2000).

Potentially more troubling still, is the possibility that habitat is generally suitable, but the adaptive traits of the fish themselves have become compromised. The demographic processes that lead to species endangerment, as well as many management activities (e.g., stocking of nonindigenous fish, artificial propagation), can quickly alter the genetic and phenotypic attributes of wild populations (Reisenbichler and Rubin 1999; Stockwell et al. 2003; Blanchet et al. 2008). Inadvertent domestication is a particularly worrisome threat to the fitness of wild populations (e.g., Araki et al. 2007). For example, Heath et al. (2003) found evidence that fecundity selection in salmon may result in contemporary evolution of egg size in hatchery populations, and egg size is a major determinant of fry size. Remediation of adaptive genetic variation presents a suite of difficult, and rarely well-informed, decisions regarding complex evolutionary interactions (Stockwell et al. 2003; Tallmon et al. 2004; Kinnison et al. 2007).

Given the somewhat different implications for management, we suggest some priority should be placed on elucidating which of these alternative explanations for such strong selection is most credible. That said, if population growth and recovery are the ultimate goal, even higher

priority might be placed on developing and testing approaches to reduce the lifetime demographic costs of strong selection, irrespective of its precise origins.

Concluding remarks

Most species conservation and restoration programs seek to preserve local adaptation, but management activities are nearly always conducted without direct insights into selectional processes that might foster or impair restoration goals (Ashley et al. 2003; Stockwell et al. 2003, 2006; Kinnison and Hairston 2007). Evolutionary biologists have developed a wide assortment of tools to assess natural selection and contemporary evolution in the wild. These tools can provide insights that are generally not revealed by the common molecular approaches that often serve as a first-cut to genetic conservation. The present research not only demonstrates that selection can be strong enough to merit attention in restoration, but that it can vary across geographic gradients relevant to current scales of management and be correlated with commonly measured habitat attributes. As such, measures of selection may afford managers with some capacity to predict, and perhaps even optimize, the performance and evolution of the stocks they manage. Importantly, the present study serves as an example that selectional assessments can be effectively implemented, even within the restrictive confines of an active endangered species program.

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