VARIATION OF AGONISTIC BEHAVIOR AND MORPHOLOGY AMONG JUVENILE CHINOOK SALMON (ONCORHYNCHUS TSHAWYTSCHA) OF HATCHERY, WILD, AND HYBRID ORIGIN UNDER COMMON REARING CONDITIONS

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A

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By

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Abstract

Hatcheries play an important role in the enhancement of Pacific salmon (genus *Oncorhynchus*) as a resource, but genetic and phenotypic divergence from wild populations may occur as a result of founder effects, genetic drift and/or domestication. In this study, agonistic behavior, ability to establish dominance, and morphology were compared among juveniles of chinook salmon (*Oncorhynchus tshawytscha*) that have experienced five generations of hatchery ranching culture, juveniles derived from the wild founding stock, and second generation hybrids of the two lines. The parent generation of all lines was cultured in the same hatchery environment as the juveniles tested. Behavioral observations were conducted in replicate artificial stream tanks; hatchery and hybrid fish were significantly more aggressive than wild derived fish. No difference was detected in the ability of fish lines to win dyadic dominance contests. Thin-plate spline analysis was used to characterize morphometric variation; hatchery and wild derived juveniles differed significantly. Canonical discriminant analysis correctly classified 88% of hatchery fish and 90% of wild derived fish. Morphologically, hybrid fish were significantly different from both hatchery and wild derived fish. These results suggest that the differences observed between lines are genetic in origin although the sources of the divergence were not conclusively identified.
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Preface

This research is part of a larger effort underway at the NOAA Fisheries Alaska Science Center Auke Bay Laboratory exploring the impacts of hatchery culture on Pacific salmon and was sponsored in part by NOAA Fisheries Alaska Science Center Auke Bay Laboratory and the Cooperative Institute for Arctic Research Cooperative Agreement No. NA17RJ1224, in part by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration Office of Sea Grant Department of Commerce grant no. NA16RG2321, and in part by the University of Alaska with funds appropriated by the state of Alaska. The protocol for this research was approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee as governed by regulations of the US Department of Agriculture and the US National Institutes of Health.

I would like to thank my advisor, Dr. William Smoker for conceiving the project and allowing me the freedom to learn and committee members Dr. Robert Fagen, for his invaluable assistance with the design and statistics behind the behavior study, and Dr. Anthony Gharrett, for keeping me honest with the genetics underlying the experiment. From, the NOAA Fisheries Auke Bay Laboratory specifically, I would like to thank John Joyce for the original initiative behind this project, and Alex Wertheimer and Frank Thrower for providing lots of helpful advice in the field. Ty Cummins of the Little Port Walter Research Station was instrumental in keeping the water flowing and fellow graduate student Erika Ammann was a very patient and dedicated research assistant. Lastly, I would like to thank my husband, Jim Wessel, for being unconditionally supportive through all the ups and downs of my graduate school experience.
General Introduction

Pacific salmon are a valuable natural resource, both economically and culturally (Groot and Margolis 1991). As many wild populations of Pacific salmon have declined in abundance, hatcheries have played an increasingly important role in the development, enhancement, and conservation of this resource. Many factors contribute to the decline in abundance, including habitat degradation, inaccessibility of spawning habitats, fluctuating ocean conditions, and exploitation of the resource. Whereas hatcheries may efficiently produce enough fish to continue harvest, questions exist about the effect of hatchery culture on the fitness of hatchery fish and their offspring, particularly in regards to the genetic effects of cultured salmonid fishes on natural populations (Hindar et al 1991, Campton 1995). Because hatchery fish have numerous opportunities to interact with wild fish once they are released, including the potential to reproduce in the wild, and because hatcheries may be used as refuges for endangered populations, it is essential to understand how hatchery culture affects these fish in relation to wild fish, and how these effects might be expressed in hybrids.

Genetic and resultant phenotypic divergence between hatchery and wild populations may be a consequence of several circumstances. Founder effects are likely if the source population is sampled in a non-random manner or if a small number of parents is used for the initial broodstock; genetic consequences of this include biased representation of the source population’s genetic profile as well as inbreeding in the hatchery population. Genetic drift can result if a small hatchery population is genetically isolated from wild populations or if hatchery mating practices are biased in some manner;
genetic consequences include loss of heterozygosity and loss of rare alleles. Finally, domestication of fish within the hatchery environment can occur if the culturing environment exerts selective pressures different than those found in the wild; genetic consequences include loss of adaptations advantageous to survival in natural environments. In all likelihood, when divergence occurs, a combination of these circumstances is responsible.

Whereas founder effects result in genetic changes directly related to the genotypes of a small number of founders and genetic drift causes random genetic divergence that may be difficult to detect phenotypically among populations, domestication leads to evolutionarily directed genetic change that may be readily detectable by characterization of phenotypes. Differences between phenotypes of hatchery and wild fish are well documented. Hatchery produced chinook salmon in New Zealand had “poorer fitness to survive” than their natural counterparts once released (Unwin 1997) and wild chinook spawners were more successful than hatchery fish (Chebanov and Riddell 1998). Captively reared adult coho salmon (O. kisutch) differed morphologically and had less successful spawners than their wild counterparts (Berejikian et al. 1997, Hard et al. 1999). Atlantic salmon (Salmo salar) of hatchery origin differed from their wild counterparts in adult body morphology, juvenile aggression, endocrinology, and heart rates (Fleming et al. 1994, Mork et al. 1999, Johnsson et al. 2001, Fleming et al. 2002, Metcalfe et al. 2003). Hatchery masu salmon (O. masu) were superior competitors to their wild counterparts in a stream (Reinhardt et al. 2001). Differences in juvenile agonistic behavior and morphology have been documented between hatchery and wild
juvenile coho salmon (Taylor 1986, Swain et al. 1991, Swain and Riddell 1990, Berejikian et al. 1999), and juvenile hatchery steelhead trout (O. mykiss) also differed in agonistic activity from their wild counterparts (Berejikian et al. 1996). Cutthroat trout (O. clarki) of hatchery origin had differing levels of aggression and chose different habitats in an artificial stream compared to their wild counterparts (Mesa 1991), and finally, hatchery rainbow trout had smaller brain structures than their wild counterparts (Marchetti and Nevitt 2003).

While evidence for a domestication effect of hatchery culture accumulates, a certain level of skepticism remains. This is due to several reasons. Firstly, hatchery fish face the same selective forces as wild fish once they are released, and the majority of a hatchery fish’s life is spent in the wild. Because of this and the high survival rates in hatcheries, it can be difficult to believe that hatchery culture could exert a significant selective pressure. Secondly, many of the studies reporting differences tested hatchery and wild fish that did not originate from the same stock. Results are therefore compromised by the fact that differences may be due to stock differences. Thirdly, many of the studies tested hatchery fish raised in the hatchery against wild fish raised in the wild. In these cases, the effects of rearing environment cannot be ruled out. Finally, in most cases sample sizes are small and the number of individual families sampled may be unclear due to logistical reasons. This introduces uncertainty into the validity of the results as applied to the general population.

This study was intended to test for phenotypic differences of a genetic nature between a hatchery stock of chinook salmon and fish derived from the wild stock of
chinook salmon which founded the hatchery population five generations ago. In addition, fish from a line of second generation hybrids between them were also tested; this allowed us to characterize how differences detected between the hatchery and wild derived fish were expressed in hybrid offspring. All lines were produced from parents cultured in the same hatchery environment and all fish tested were raised in the same hatchery environment. Finally, equal numbers of individuals (18 for behavior; 10 for morphology) from equal numbers of families (5 for all tests) from each fish line (3 for all tests) were tested. Although the number of families tested was small, a balanced, nested design allowed us to test for family effects as well as the effect of line.

Because behavior has a direct effect on fitness and can be among the first traits affected by domestication (Olla et al. 1998) and techniques of study are well developed, we looked for differences in agonistic behavior between the hatchery and wild lines. Also, because levels of aggression in salmonids have been positively associated with dominance (Egglishaw 1967, Fenderson and Carpenter 1971, Holtby et al. 1993, Berejikian et al. 1996) and dominant individuals tend to obtain more profitable stream positions (Fausch 1984, Metcalfe 1986), the ability of hatchery fish and the hybrids to establish dominance over the wild fish was tested to determine the real world impact of any agonistic behavioral differences.

Changes in morphological traits, such as body size and shape, can also occur relatively quickly during domestication (Taylor 1986, Taylor and Larkin 1986) and body morphology can have a direct influence on an animal’s ability to exploit its natural environment (Riddell and Leggett 1981, Webb 1984a, Webb 1984b). For example, a
more streamlined body may enhance prolonged swimming ability and thus benefit fish moving in schools whereas a deeper body shape may enhance the burst swimming important in predator avoidance and capturing drift food in streams (Taylor and McPhail 1985a, 1985b, Swain and Holtby 1989). Because of this we also tested for differences in body shape between the hatchery and wild lines.
Variation of Agonistic Behavior among Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) of Hatchery, Hybrid, and Wild Origin

Abstract

Juveniles in a hatchery stock of chinook salmon that has experienced five generations of hatchery culture were significantly more aggressive than juveniles derived from the wild founding stock but produced from parents cultured in the same hatchery environment as the hatchery stock. During 20 minutes of observation in replicate artificial stream tanks, hatchery fish made significantly greater numbers of charges, displays, and nips than wild derived fish. Second generation hybrids between the two lines also made significantly greater numbers of charges, displays, and nips than wild derived fish but made significantly fewer displays than hatchery fish. Equal numbers of parr (18) from equal numbers of families (5) from each fish line (3) were tested and all lines were raised in a similar hatchery environment. These results suggest that the differences detected are genetic in origin and are consistent with divergence of the hatchery stock from the founding wild stock. No difference was detected in the ability of fish lines to win dyadic dominance contests.

Introduction

Pacific salmon (genus *Oncorhynchus*) are a valuable natural resource, both economically and culturally (Groot and Margolis 1991). Many wild populations of Pacific salmon have declined in abundance and hatchery production has played an increasingly important role in the development and enhancement of this resource. A number of factors are responsible for this decline, including habitat degradation, inaccessibility of spawning habitats, fluctuating ocean conditions, and exploitation of the resource. Although hatcheries may efficiently produce enough fish to continue harvest, questions exist about the effect of hatchery culture on the genetic fitness of hatchery fish and their offspring (Hindar et al 1991, Campton 1995). Because hatchery fish have numerous opportunities to interact with wild fish once they are released, including the potential to reproduce in the wild and mate with wild fish, and because hatcheries may be used as refuges for endangered populations, it is essential to understand how hatchery culture affects these fish in relation to wild fish, and how these effects might be expressed in hybrids.

Hatchery populations may diverge genetically from wild populations as a result of a small number of founding parents (founder effect), through genetic isolation of a small population in the hatchery (genetic drift), adaptation to the novel hatchery environment (domestication), or through manipulation by humans (domestication/artificial selection). While evidence of a founder effect and genetic drift may lie hidden in the genotypes of the population and may not reflect fitness differences between populations, evidence of domestication may be observed in the phenotypic expression of fitness related traits.
Although evidence for a domestication effect from hatchery culture has accumulated, a certain level of skepticism remains. This is due to several reasons. Firstly, hatchery fish face the same selective forces as wild fish once they are released, and the majority of a hatchery fish’s life is spent in the wild. Because of this and the high survival rates in hatcheries, it can be difficult to accept that hatchery culture could exert a significant selective pressure in a few generations. Secondly, many of the studies reporting differences tested hatchery and wild fish that did not originate from the same stock. Results are therefore compromised by the fact that differences may be due to stock differences. Thirdly, many of the studies tested hatchery fish raised in the hatchery against wild fish raised in the wild. In these cases, the effects of rearing environment cannot be ruled out. Fourthly, in most cases sample sizes are small and the number of individual families sampled may be unclear due to logistical reasons. This introduces uncertainty into the validity of the results as applied to the general population. Finally, if genetic divergence is demonstrated between hatchery and wild populations, it can be difficult to delineate between founder effects, genetic drift, or domestication as the cause.

Behavior can be among the first traits affected by domestication (Olla et al. 1998) and differences in behavior between hatchery and wild fish are well documented. These changes tend to occur in the frequency and intensity of expression of behaviors rather than the behavioral pattern itself (Ruzzante 1994). For example, differences exist in agonistic behavior between hatchery and wild salmonids of several species including coho salmon (O. kisutch; Taylor 1986, Rosenau and McPhail 1987, Swain and Riddell 1990, Berejikian et al. 1999), Atlantic salmon (Salmo salar; Mork et al. 1999, Johnsson
et al. 2001, Metcalfe et al. 2003), steelhead trout (*O. mykiss*; Berejikian et al. 1996), and cutthroat trout (*O. clarkii*; Mesa 1991). In addition, hatchery masu salmon (*O. masu*) were superior competitors to their wild counterparts in a stream (Reinhardt et al. 2001).

Although differences in agonistic behavior have been documented between juvenile chinook salmon from stream-type and ocean type populations (Taylor and Larkin 1986, Taylor 1988) they have not been documented between juvenile chinook salmon of hatchery and wild origin. The two “types” of chinook salmon are distinguished primarily by the length of time juveniles spend in freshwater before migrating to sea; the “stream-type” spend one or more years in freshwater while the “ocean-type” migrate to sea during their first year of life, normally within three months after emergence. Populations of fish characterized by longer freshwater residencies tend to be more aggressive (Taylor and Larkin 1986) possibly because agonistic behavior benefits fish in competition for food and space; levels of aggression in salmonids have been positively associated with dominance (Egglisheaw 1967, Fenderson and Carpenter 1971, Holtby et al. 1993, Berejikian et al. 1996), and dominant individuals tend to obtain more profitable stream positions (Fausch 1984, Metcalfe 1986).

This study was intended to test for baseline within-population differences in agonistic behavior between juveniles originating from a hatchery population of chinook salmon and juveniles derived from the same wild stock that founded the hatchery population five generations previously. We also looked at second generation hybrids between the two lines to determine how any difference detected might be expressed in hybrid offspring between wild and hatchery fish. In addition, the ability of hatchery fish
and the hybrids to establish dominance over the wild fish was tested to determine the real world impact of any agonistic behavioral differences.

Materials and Methods

Study Population

A stock of “stream-type” chinook salmon cultured at the NOAA Fisheries Research Station at Little Port Walter Alaska was used in this study. The original hatchery population was established in 1976 using gametes from 6 females and 8 males collected from the Chickamin River which is located on the mainland of Southeast Alaska (see Hard et al. 1985). The majority of fish in this stock of chinook salmon mature at age 5 although some return at age 6 and a few males return at age 4. In 1996, approximately 4 chinook salmon generations after the original hatchery stock was established, gametes were collected from 5 females and 11 males captured in the same area of the Chickamin River. A pure “wild” line was established with the gametes from 5 wild males and 5 wild females and a hybrid line was established with gametes from hatchery females, gametes from the same 5 wild males used to establish the “wild” line, and gametes from 6 additional wild males. All lines of chinook salmon released from Little Port Walter are marked with group specific coded wire tags, which are decoded before spawning the next generation.

In 2002, adult salmon progeny from the hatchery, “wild”, and hybrid lines returned to the hatchery and were spawned to continue the hatchery and wild derived lines and produce second generation hybrid crosses with the hatchery line. All lines were
raised at Little Port Walter using standard hatchery techniques in which juveniles spend over one year in culture, smolts are released to sea, and all freshwater life stages from spawning onward are artificially controlled: environmental rearing differences between lines were thus minimized.

In conjunction with another study, parentage analysis was performed on all "wild" adult spawners in order to ensure that inbreeding did not occur; this allowed us to determine the relatedness of all the wild families under the assumption that the original 16 adults collected in 1996 were not related. All wild families tested in this study were related, ranging from cousins to double cousins to half-sibs (Figure 1). Although parentage analysis was not performed for hybrid fish, the small number of wild adults used in 1996 indicates that second generation hybrid families tested may be inbred and have an unknown degree of relationship with each other, ranging from unrelated to half cousins to double half cousins. In addition, second generation hatchery wild hybrids tested have an unknown degree of relationship with the wild derived families tested, ranging from unrelated to half cousin to double half cousin. Finally, the small number of founders used for the establishment of the hatchery population in 1976 indicates that founder effect and genetic drift will have significant influence over the genetic dynamics of this population.

Five individual families from the hatchery line, five from the wild line, and five from the second generation hybrid line were tested. Within each line, two families shared a sire (half-sibs) and relatedness beyond this was not determined except as detailed above. Individual fish were randomly selected shortly after ponding; an entire family
was placed into a 10 liter tray and a small dip-net was used to capture 2 or 3 fish at a time without conscious selection until a total of 60 fish from each family was attained. Each of the 15 families was separately raised in micro vertical raceways (see Heintz and Joyce 1992). Fish were fed commercial fish food several times daily according to the manufacturer’s instructions.

Stream Tanks

All experiments were conducted in the behavior lab at Little Port Walter (Figure 2). This lab consists of two flumes approximately one meter wide by eight meters long. The flumes have 10 glass windows for observation on each side. Each flume contains ten standard 55-gallon aquaria, situated 2 wide by five long. Each aquarium has two water inflows upstream and two siphons (outflows) at the downstream end. Water is provided from a head tank which is supplied by a line originating in Sashin Lake, a local lake that supports a population of rainbow trout (O. mykiss). The flumes provide a water bath for the aquaria. Standpipes in the flumes maintain water levels. The aquaria are graveled and equipped with upstream mid-water feeders. Light is provided by a bank of 5 standard pairs of fluorescent lights over each flume. Flumes are covered by black plastic sheeting to minimize disturbance of fish during observation.

Agonism Experiment

Agonism experiments were conducted in the stream aquaria. Water inflow was maintained between 7.5 and 9.4 liters per minute. Water temperature averaged 14.0° C ±0.60. Water depth was 25 cm and the light schedule was 16h light:8 h dark to mimic the
natural light rhythm. A mixture of approximately 113 frozen daphnia and 17 frozen bloodworms was provided through the midwater upstream feeders four times daily. Two size matched fish (within 3 mm, mean size of all fish throughout the experiment = 73mm +/- 4.5mm) of non-sib families from a single fish line were placed into each of 15 tanks (five tanks per line). Size matching was accomplished by randomly choosing a fish from one family and subsequently picking a fish that appeared to be closely matched in size from the second family. Occasionally a second or third fish needed to be chosen from the second family in order to accomplish the size match. All families were equally represented throughout the experiment. In order to distinguish between fish in a tank, one fish was marked with an adipose fin clip. In order to minimize clip effect differences, scissors were also run over the back of the non-clipped fish. Fish were anesthetized with MS-222 (Tricaine methansulfonate) prior to measuring and marking; they were then placed in individual five gallon buckets and allowed to recover from the stress of handling overnight.

The following afternoon pairs were placed in the aquaria and food was provided after an acclimation period of three hours. The fish were fed twice the next morning and monitored to assure that they were feeding. After 24 hours in the aquaria observations were conducted for 10 minutes on each tank. Food was introduced at the beginning of each observation, and behaviors (Table 1) were recorded individually for each fish using the event recording software JWatcher® (2000, D.T. Blumstein, C.S. Evans and J.C. Daniel; available at http://galliform.psy.mq.edu.au/jwatcher). Individual behaviors were scored with a keystroke as they occurred, and behaviors recorded for duration were
scored with a keystroke as they began and another keystroke when they ended; an internal clock within the software recorded the time of the keystroke as well as the time between keystrokes. Food was provided once more that day after observations, then once again the following morning at least one hour before a second set of observations. The second set of observations was conducted approximately 18 hours after the first set of observations in an identical manner. A total of 9 trials of 15 tanks each were run, resulting in a sample size of 45 tanks or 90 fish for each line and a sample size of 18 observations for each of the 15 families. The experiment ran between the 21st of July and the 7th of August, 2003.

Dominance Experiments

After use in the agonism experiments, five pairs of wild-derived and hatchery or hybrid fish were matched according to size and differing adipose clip and placed into stream aquaria in the afternoon. Adipose clips between types were balanced over the length of the experiment such that half of the wild-derived fish were clipped and half of the challenging fish were clipped. Fish were allowed to acclimate for 44 hours before observation and fed in the same manner as the agonism experiment; once the first evening, four times the following day, and twice on the observation day. Dominance was assessed by observation of the fish for 10 minutes immediately after feeding. A fish scored as dominant if it fed more, initiated the majority of aggressive interactions, and occupied the more advantageous upstream position. Similarly, a fish was scored as subordinate if it fed less, rarely initiated aggressive interactions, and typically occupied marginal positions close to the bottom or along the tank edges. A secondary dominance
assessment was conducted one hour later to confirm that the same fish still occupied the dominant position. Eight trials of five tanks were run, resulting in 20 tanks of wild derived vs. hybrid and 20 tanks of wild derived vs. hatchery. These trials ran between the 23rd of July and the 7th of August, 2003.

To increase power, additional trials were run with fish that were not used in the agonism experiments. These fish were anesthetized with MS-222 (Tricaine methansulfonate), measured, half were marked with an adipose fin clip and all were placed individually in 5 gallon buckets to recover overnight. Adipose clips were again balanced between lines. The following afternoon, pairs of size matched fish were placed in the stream aquaria and fed in the same manner as the agonism experiment. After 44 hours in the tanks dominance was assessed primarily and secondarily in the same manner as the original dominance experiment. Two trials of 20 tanks were run resulting in 20 additional trials each of the wild derived vs. hatchery and wild derived vs. hybrid contests for an overall sample size of 40 for each. These trials ran between the 10th and 13th of August, 2003.

**Statistical Analysis**

Counts of individual behaviors and durations of individual behaviors were summed for each fish over the length of observation periods for statistical analysis. In addition, all aggressive behaviors were summed together for individual fish to create an additional variable of total aggressive behavior (TAG) for both counts and durations. A generalized linear model was used for analysis of behavioral count data, which exhibited an over-dispersed poisson distribution, with family = quasi-likelihood, link = log and
variance = mu. Behavior duration data was log transformed to achieve normality and was then tested with analysis of variance (ANOVA). Behavior proportions were produced by dividing individual behavior counts by total aggressive behavior counts for each individual fish. These proportions and the proportion of time fish spent within one body length of each other were transformed by arcsine to achieve normality and tested with ANOVA. Effects of line of origin, family within line of origin, adipose clip, and the interaction of adipose clip and line of origin were tested. Two models were tested, a full model and a reduced model as follows:

\[ Y_{ijkl} = \mu + L_i + F_{ij} + C_k + C_k \times L_i + e_{ijkl} \]  \hspace{1cm} (1)

\[ Y_{ij} = \mu + L_i + e_{ij} \]  \hspace{1cm} (2)

where \( Y_x \) is the behavioral response expressed as count, duration, or proportion, \( \mu \) is the theoretical population mean, \( L_i \) is the effect of line of origin, \( F_{ij} \) is the effect of family nested within line of origin, \( C_k \) is the effect of adipose clip, \( C_k \times L_i \) is the effect of the interaction of clip and line of origin, and \( e_x \) is the random error. As the data from the two separate 10 minute observations did not significantly differ after preliminary analysis, they were combined for final analysis.

For the dominance challenges, number of successes (dominance) for each challenging line (hatchery or hybrid) was analyzed using the exact binomial test with the hypothesized proportion at 0.5 and a two-sided alternative hypothesis. All statistical tests were performed using the S-plus statistical software package (version 6.0, Insightful Corp.).
Results

All fish appeared to acclimate well and were feeding on the daphnia/bloodworm mixture by the second feeding. Before the addition of food, fish were typically either actively exploring the aquarium or at rest in the downstream third. Upon addition of food at the beginning of the observation at least one of the fish pair would usually begin actively feeding while the other fish would not feed at all or fed occasionally by darting for food. Occasionally both fish actively fed. Agonistic behavior would typically occur at this time and continue or increase as food abundance decreased. Typically, one of the fish was more active, held a more profitable stream position after addition of food, and initiated a majority of the agonistic interactions. Occasionally few or no agonistic interactions occurred.

The full statistical model and the reduced statistical model were tested on all behavioral data recorded except for length of time spent within one body length of another fish for which the reduced model alone was tested. All tests of the full model revealed no significant effect of family nested within line of origin, clip, or clip and line of origin interaction. Likelihood ratio tests between the full model and reduced model similarly revealed no significant differences between the models; for that reason only the results of the reduced model are reported here.

Hatchery and hybrid fish exhibited significantly greater numbers of total aggressive activity against fish from the same line than wild derived fish (Figure 3, Table 2). Broken down into individual behaviors, hatchery and hybrid fish performed significantly more charges and nips than wild fish. Additionally, hatchery fish performed
the most displays while wild fish performed the least number and hybrid fish performed an intermediate number significantly different than both the hatchery and wild derived lines (Figure 3, Table 2). There were no significant differences between lines in the number of foodstrikes made.

Duration data was consistent with the count data. Hatchery and hybrid fish spent significantly more time on total aggressive activities than wild derived fish \( (F=6.46, \ df=2,267, \ p=0.002) \). For individual behaviors, hatchery and hybrid fish spent significantly more time charging \( (F=6.07, \ df=2,267, \ p=0.003) \) and displaying \( (F=10.44, \ df=2,267, \ p=<0.001) \) than wild derived fish (Figure 4).

Differences were also displayed in the relative frequencies of aggressive behaviors. Approaches \( (F=5.99, \ df=2,267, \ p=0.003) \) contributed a significantly higher proportion to total aggressive behaviors of wild derived fish than hatchery or hybrid fish. Displays \( (F=5.08, \ df=2,267, \ p=0.007) \) contributed a significantly higher proportion to aggressive behaviors of hatchery fish than wild derived fish while hybrid fish performed an intermediate proportion not significantly different than the hatchery or wild derived lines. Hybrid fish performed a higher proportion of charges \( (F=5.36, \ df=2,267, \ p=0.005) \) than wild derived fish while hatchery fish performed an intermediate proportion not significantly different than the hybrid or wild derived lines (Figure 5). Finally, hatchery fish spent a significantly greater proportion of time within one body length of each other than either hybrid or wild derived fish (Table 3).

No significant difference in the ability of wild derived fish and hybrid or hatchery fish to dominate was detected (Table 4). Typically dominance was established by the first
observation period and remained unchanged through subsequent observations. Occasionally there was no apparent dominance relationship during the first observation; in these cases, a second observation was made several hours later and in all of these cases a dominant fish was identified and confirmed with a third observation.

Discussion

The demonstration of behavioral differences between juveniles from a hatchery stock of chinook salmon and juveniles derived from their wild stock founder population is consistent with the occurrence of domestication. No effect of family was detected in any of the behavioral traits, strengthening the likelihood that the observed differences are due to divergence between lines rather than differences between families. Because all fish tested were raised in similar hatchery environments these differences are likely genetic, rather than environmental, in origin.

Several factors confound the results of this study. The fact that the original hatchery stock was established from just 6 females and 8 males collected at one time from one area on the Chickamin River indicates that a founder effect may influence the genetic dynamics of the hatchery population. It is likely that the original broodstock was representative of just a small portion of the genetic variation contained in the wild population; furthermore, although the number of breeders in the hatchery population has been high in subsequent generations, it is likely that inbreeding occurred. Because random genetic drift has most certainly occurred in the hatchery population and because the original broodstock may not have been representative of the wild population, genetic differences would almost certainly be expected between the hatchery population and a
population newly derived from the wild founding population. Further complicating
matters, the 1996 sampling again included very few adults, 4 females and 4 males,
collected at one time from one area of the Chickamin River. Again, these fish most likely
represent a small portion of the genetic variation found in the wild. Genetic differences
would certainly be expected between fish derived from this group of wild fish and the
hatchery population established in 1976. Finally, because of logistical constraints, only
five families from each line (hatchery, hybrid, and wild derived) were tested.

These three issues, hinging on the question of whether a small number of fish are
representative of the larger population, call into question the validity of the results as
applied to hatchery and wild populations in general and as applied to the populations
from which the families were drawn. However, in this study, family did not have a
statistically detectable effect on aggressive behavior; this may indicate that aggressive
behavior has a low heritability and thus for this trait, family level variation may be
representative of the variation present in the population. Finally, founder effect and
genetic drift result in random genetic divergence between populations. The traits tested
for in this study are fitness related and are expected to be under selective pressure;
random genetic changes would not necessarily impact them. In fact, a simulation was run
to determine if the observed differences between wild derived and hatchery derived
juveniles could be reasonably expected to occur under natural selection. Log(duration) of
total aggressive activity was used in the simulation because this was the most normally
distributed parameter observed. The mean and standard deviation of generation 0 was set
equal to that observed in the wild derived juveniles (2.76, 1.60) and the change in
log(duration) of total aggressive activity was calculated according to the following equations:

\[ h^2 \frac{\bar{x}_{progeny}}{\bar{x}_{breeders}} \frac{\bar{x}_{population}}{\bar{x}_{population}} = \frac{R}{S} \frac{\frac{R}{\hat{s}_{population}}}{\frac{S}{\hat{s}_{population}}} \]  \hspace{1cm} (3)

where \( h^2 \) is the heritability of the trait being tested, \( \hat{s} \) is the standard deviation and

\[ \frac{R}{\hat{s}_{population}} \frac{S}{\hat{s}_{population}} h^2 i^* h^2 \]  \hspace{1cm} (4)

where \( i \) is the selection intensity, and when selection intensity is constant over several generations (\( n \)) the overall standardized response is

\[ \frac{R}{\hat{s}_{population}} n^* i^* h^2 \]  \hspace{1cm} (5)

\[ i = \frac{z}{p} \]  \hspace{1cm} (6)

where \( p \) is the proportion selected and \( z \) is the \( f(x) \) intercept for the truncation point, and

\[ z = \frac{1}{\sqrt{2}} e^{-\frac{x^2}{2}} \]  \hspace{1cm} (7)

where \( x \) is the location of the truncation point on the \( x \)-axis. Running the simulation for 5 generations using a low heritability (0.1) and a reasonable selected proportion of 50% resulted in a change in mean log(duration) of total aggressive activity (from 2.76 in generation 0 to 3.39 in generation 5) very similar to the difference observed between the wild derived (2.76) and hatchery (3.47) fish. Several other combinations of heritability
and selected proportion had similar outcomes including a heritability of 0.2 paired with proportions of 70% (3.32) and 80% (3.55) and a heritability of 0.1 paired with proportions of 60% (3.28) and 40% (3.53). Nonetheless, it is still possible that the few original founders of the hatchery population were more aggressive than the general population and that this is the basis of the observed differences.

An added concern is the known relatedness of the wild-derived families and the unknown relatedness of the hybrid and hatchery families. Siblings may be less aggressive towards each other than non-related fish (Brown and Brown 1993, 1996) although this same observation has not been made for relationships extending beyond full-sib; in fact related fish may not even recognize each other unless they are raised in a common environment (Courtenay et al. 1997, 2001). Because the closest possible relationship of the fish tested together in this study was double-cousin, and because the families were all raised separately, it is unlikely that kinship played a role in the aggressive interactions observed between these fish.

Families from this stock of hatchery chinook salmon and families from second generation hybrids with the wild founder population were more aggressive than families derived from the wild founder population. These results are consistent with other studies that observed that hatchery salmonids were more aggressive than wild fish (Moyle 1969, Swain and Riddell 1990, Mesa 1991). The aggressive nature of a fish is a trait directly related to survival in the wild through competition for food and space. In natural environments there is a trade off between vigilance for predators and other activities such as agonistic interactions and foraging (Olla et al. 1998). In the hatchery environment, the
selective pressure of predation is removed and increased aggressiveness may be favored in hatchery juveniles. More aggressive dominant fish may behaviorally suppress or actively inhibit feeding in subordinate fish (Magnuson 1962, Fenderson et al. 1968, Koebele 1985). Faster growth may thus be a benefit of being among the more aggressive fish, and once salmonids have smolted, the largest fish may have the highest survival (Holtby et. al 1990, Henderson and Cass 1991, Koenings et. al 1993). Additionally, artificial spawning in the hatchery environment removes the selective pressure for social behavior characteristics important for successful spawning in nature and this may influence behavior of subsequent generations.

Second generation hybrids of the hatchery and wild fish more closely resembled the hatchery fish, although they also exhibited some behaviors intermediate between the hatchery and wild derived lines. The resemblance between the hatchery and hybrid fish may be due to the fact that all fish were raised in a hatchery environment and tested in an artificial stream; it is likely that social behaviors would change in a natural environment and possible that the second generation hybrids would more closely resemble the wild fish in this case. The fact that second generation hybrids also displayed some intermediate values suggests that if domestication occurs, it may be mitigated by outbreeding with wild fish. A more comprehensive study should demonstrate how these behavioral differences would be expressed in a natural environment since this is where both ecologically important interactions and possible interbreeding between hatchery and wild fish could occur. The increased aggressiveness of the hatchery and hybrid fish in this study did not translate into an enhanced ability to dominate the wild fish in dyadic
contests nor did the fish from the more aggressive lines consume more food, suggesting that the elevated levels of aggression may be ecologically insignificant.

Additional studies characterizing domestication differences between hatchery and wild populations of salmonids should attempt to verify that the hatchery populations tested are not suffering from excessive inbreeding or founder effects that may contribute to divergence not attributed to domestication effects. Furthermore, attempts should be made to test a sufficient number of families from both the wild and hatchery populations to strengthen the likelihood that any differences observed are indicative of real differences between populations. Nonetheless, although this study is unable to delineate between founder effects, genetic drift, and domestication as the underlying cause for the differences observed in aggressive activity, the results add to a growing body of evidence suggesting that hatchery culture imposes a domestication effect on cultured salmonids resulting in a genetically based behavioral divergence from their wild counterparts. While these differences may be attributable to a combination of founder effect and genetic drift, they are consistent with the expectation of behavioral differences imposed by domestication; prudent interpretation of these results includes domestication as a possible cause. The hatchery stock of chinook in this study has experienced hatchery culture for only five generations and the fact that behavioral differences exist indicates how rapidly domestication selection can occur despite lack of intention.

It is unclear how detrimental these effects could be in wild populations. Consequences of increased aggressive activity in a natural environment could include compromised predator avoidance capabilities (Olla et al. 1998). If the hatchery
environment inadvertently selects for the greater body size or higher metabolic rate that could result from aggressive or competitive interactions (Ryer and Olla 1995, 1996), fish may need to forage at increased risk from predators (Johnsson 1993). In fact, juvenile hybrids of steelhead and domesticated rainbow trout were more willing to risk exposure to a predator than were juvenile steelhead, even though they were equally susceptible to the predator (Johnsson and Abrahams 1991). In addition, a fish that spends an inordinate amount of time on aggressive behaviors may be less vigilant for predators or may even be targeted by predators because they are more conspicuous (Olla et. al 1998). It is clear that hatchery technologies need to continue to be further developed in order to minimize the negative effects of culturing.

Acknowledgments

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Figure 1.1. Known relatedness of wild derived families; letters represent five wild derived families, solid line represents half-sib families, dotted lines represent cousin relationships, and dashed and dotted lines represent double-cousin relationships.
Figure 1.2. Diagram of behavior lab showing one side of one flume (a) and details of one artificial stream tank. Light is provided by a bank of 5 standard pairs of fluorescent lights over each of 2 flumes. Flumes are covered by black plastic sheeting to minimize disturbance of fish during observation. Arrows indicate direction of water flow. Detailed parts include the main water supply line to all tanks in a single flume (b), 2 funnels through which food is provided without disturbing the fish (c), 2 mid-water inlets for water and food (d), siphon outlet for water (e), standpipe regulating water depth in all tanks in a single flume (f), and indication of water depth in tank (g).
Figure 1.3. Mean number of occurrences of selected aggressive behaviors and total aggressive (TAG) activity during 20 minutes of observation for hatchery (HH), hybrid (HW), and wild (WW) fish. Significant differences are indicated by differing letters over the bars. Error bars are 95% confidence intervals generated by 1000 bootstrap replications of the data. See Table 2 for associated statistics.
Figure 1.4. Mean of the logs of the durations of selected aggressive behaviors during 20 minutes of observation. Significant differences between fish lines are indicated by differing letters over the bars. Error bars are 95% confidence intervals generated by 1000 bootstrap replications of the data. See text for associated statistics.
Figure 1.5. Proportions of aggressive behaviors performed; graphs show the relative contributions of each type of aggressive behavior to overall aggressive activity for hatchery, hybrid, and wild fish. Significant differences in relative frequencies of behaviors between fish lines are indicated by differing letters next to behaviors. See text for associated statistics.
Table 1.1. Descriptions of behaviors recorded for fish during 20 minutes of observation.

All behaviors were recorded for occurrence and duration except nip and foodstrike which were recorded for occurrence only and location which was recorded for duration only

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Display</td>
<td>Extended dorsal and anal fins, opening of the mouth, a stiffening of the body with an accentuated swimming motion, and possible “quivering”</td>
</tr>
<tr>
<td>Approach</td>
<td>An intentional movement towards another fish</td>
</tr>
<tr>
<td>Charge</td>
<td>Swimming with increasing velocity directly at another fish</td>
</tr>
<tr>
<td>Chase</td>
<td>One fish pursues another fish past the point from where the chased fish was originally stationed</td>
</tr>
<tr>
<td>Nip</td>
<td>A bite directed toward or physically touching another fish</td>
</tr>
<tr>
<td>Foodstrike</td>
<td>A fish physically captures and handles a food item</td>
</tr>
<tr>
<td>Location</td>
<td>Fish either within one body length of each other or farther than one body length from each other</td>
</tr>
</tbody>
</table>
Table 1.2. Mean counts of behaviors observed during 20 minutes of observation for hatchery, wild derived, and hybrid fish and statistical results from the generalized linear model function in S-plus (version 6.0, Insightful Corp.) with family = quasi-likelihood, link = log and variance = mu. Tests were performed for the effects of type, clip, and their interaction. No significance was found for clip or the clip:type interaction so these factors were dropped from further analyses.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Hatchery (standard error)</th>
<th>Wild Derived (standard error)</th>
<th>Hybrid (standard error)</th>
<th>F</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Display</td>
<td>14.33 (±1.170)</td>
<td>8.46 (±0.915)</td>
<td>11.10(±0.906)</td>
<td>5.40</td>
<td>2,267</td>
<td>0.005</td>
</tr>
<tr>
<td>Approach</td>
<td>6.33 (±0.634)</td>
<td>5.70 (±0.522)</td>
<td>6.07 (±0.537)</td>
<td>0.32</td>
<td>2,267</td>
<td>0.727</td>
</tr>
<tr>
<td>Charge</td>
<td>2.10 (±0.548)</td>
<td>0.70 (±0.216)</td>
<td>2.46(±0.514)</td>
<td>8.66</td>
<td>2,267</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Chase</td>
<td>1.08 (±0.334)</td>
<td>0.61 (±0.215)</td>
<td>1.14(±0.300)</td>
<td>1.13</td>
<td>2,267</td>
<td>0.324</td>
</tr>
<tr>
<td>Nip</td>
<td>2.67 (±0.654)</td>
<td>0.83 (±0.225)</td>
<td>2.11(±0.411)</td>
<td>5.29</td>
<td>2,267</td>
<td>0.006</td>
</tr>
<tr>
<td>TAG</td>
<td>26.51 (±2.619)</td>
<td>16.30 (±1.444)</td>
<td>22.88(±1.951)</td>
<td>6.86</td>
<td>2,267</td>
<td>0.001</td>
</tr>
<tr>
<td>Foodstrike</td>
<td>42.30(±4.923)</td>
<td>37.00(±3.848)</td>
<td>44.08(±4.102)</td>
<td>0.74</td>
<td>2,267</td>
<td>0.476</td>
</tr>
</tbody>
</table>
Table 1.3. Mean percent of time spent within one body length for 2 hatchery, hybrid or wild fish during 20 minutes of observation. Data was tested for significance by transforming by arcsine and testing with one-way analysis of variance.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Percent of Time (standard error)</th>
<th>F</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery</td>
<td>45</td>
<td>30.7% (±2.77)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hybrid</td>
<td>45</td>
<td>16.7% (±1.90)</td>
<td>13.240</td>
<td>2,132</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Wild</td>
<td>45</td>
<td>16.6% (±1.95)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1.4. Results of dominance contests between wild and hatchery or hybrid fish.

<table>
<thead>
<tr>
<th>Winner</th>
<th>n</th>
<th>Hatchery</th>
<th>Hybrid</th>
<th>Wild</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wild vs. Hatchery</td>
<td>40</td>
<td>21</td>
<td>n/a</td>
<td>19</td>
</tr>
<tr>
<td>Wild vs. Hybrid</td>
<td>40</td>
<td>n/a</td>
<td>20</td>
<td>20</td>
</tr>
</tbody>
</table>
References


Taylor, E.B., and P.A. Larkin. 1986. Differences in morphology between wild and hatchery populations of juvenile coho salmon. Prog. Fish-Cult. 48:171-176
Abstract

Body morphology differed significantly between juvenile hatchery chinook salmon that have experienced five generations of hatchery culture and juveniles produced from parents cultured in the same environment but derived from the wild founding stock. All lines tested were raised in a similar hatchery environment. Thin-plate spline analysis was used to characterize the morphometric variation among these lines of fish. Hatchery fish had a more compressed body, a narrower head, shorter maxillae, and a longer and narrower caudal peduncle than wild fish. Canonical discriminant analysis was able to correctly classify 88% of hatchery fish and 90% of wild fish. Second generation hybrids of the two lines were morphologically intermediate to but significantly different from both the hatchery and wild lines, and they appeared to be more similar to the wild line. These results suggest that the differences observed between lines are largely genetic in origin and may be a result of divergence of the hatchery stock from the founding wild stock.

Introduction

Because Pacific salmon home to population specific spawning streams, genetic isolation occurs, resulting in genetic divergence among populations. This divergence may be reflected in morphological differences among populations. While these differences are obvious between different species occupying very diverse environments, intraspecific differences may be difficult to characterize. Because the body shape of a fish affects how it moves through its aquatic environment and thus how well it will be able to feed and avoid predation, selection pressure has resulted in differing optimal body forms of fish living in differing environmental niches (Webb 1984a, Webb 1984b). Hatchery rearing exposes juvenile salmonids to novel environmental conditions very different than those found in the wild. Some of these differences include a lack of predators, an abundance of food, and a lack of structure resulting in uniform water flow. Because body form is an adaptive trait, these altered developmental and evolutionary forces may cause hatchery fish to diverge phenotypically and genetically from wild fish.

Several studies have attempted to characterize morphological differences between wild populations of salmon as well as between wild and hatchery populations. Different morphological body forms and functional differences in swimming performance have been defined for interior and coastal populations of juvenile coho salmon (*Oncorhynchus kisutch*) (Taylor and McPhail 1985a, Taylor and McPhail 1985b). These differences were inherited and appear to be adaptive; interior populations had more streamlined bodies and better prolonged swimming performance than coastal populations which had deeper, robust bodies and better burst swimming performance. These interpopulation trends in
body morphology were also evident in a small number of adult fish examined. Morphological differences were also observed in juvenile coho rearing in a lake and its tributary stream (Swain and Holtby 1989). The lake fish were more streamlined and appeared to be adapted to prolonged swimming and schooling while the stream fish were deeper bodied and appeared to be better adapted for burst swimming. Chinook salmon \( (O. \text{tshawytscha}) \) juveniles differed morphologically in association with life history types that reared in dissimilar environments (Carl and Healey 1984) and Atlantic salmon \( (Salmo \text{salar}) \) differed morphologically based on differing environments in their wild rearing streams (Riddell and Leggett 1981). Differences in morphology between wild and hatchery populations of juvenile coho salmon were attributed primarily to environmental differences (Taylor 1986), although another study demonstrated a genetic component (Swain et al. 1991). Although the velocity of water flow directly affects the phenotypic expression of morphology in juvenile salmon (Pakkasmaa and Piironen 2001), substantial genetic influence over variation in body size and components of shape occurs in juvenile hatchery chinook salmon (Hard et al. 1999). These studies suggest that both environment and genetics play an important role in the development of body form.

Wild populations of salmonids appear to be morphologically adapted to the selective pressures of their rearing environments. Hatchery salmonids, in turn, may be morphologically adapted to the hatchery environment. Although the plasticity and functional significance of these morphological phenotypes are not well defined, these adaptations are likely under some genetic control. Because hatchery salmonids interact with wild fish in their natural environment and may even breed both alongside and with
them it is important to understand divergence that may occur in hatchery populations.
The objective of this study was to determine if morphological differences of a genetic
nature exist between juveniles in a hatchery stock of chinook salmon that has experienced
five generations of hatchery culture and juveniles derived from the wild founding stock.
A secondary objective was to characterize how any differences might be expressed in
second generation hybrids of the two populations.

Variation in body form can be complex and difficult to quantify. Traditional
methods involve lists of measured linear distances (trusses) between pairs of identifiable
landmarks while newer methods involve the geometric locations of landmarks
represented as Cartesian grid coordinates (Parsons et al. 2003). Thin-plate spline (TPS)
analysis of the geometric coordinates allows the deformation in shape of one specimen in
relation to another to be mapped (Bookstein 1991). A comparison of thin-plate spline
analysis to the more traditional truss based methods revealed that the TPS method yielded
stronger evidence of morphological differences among species of new world cichlids
(Parsons et al. 2003). Additionally, the deformation grids yielded by the TPS method
provided clear and visually interpretable figures that facilitated analysis of body form.
The application of geometric methods is becoming easier with the availability of user
friendly freeware computer programs. In this study we use TPS analysis of the geometric
coordinates of 13 landmarks on the juvenile fish to characterize the morphometric
variation in the wild and hatchery fish and their second generation hybrids.

Free software programs to perform geometric analyses (including TpsDig, TpsRelw,
TpsRegr used here) are available through the morphometrics website at the State
University of New York at Stony Brook: http://life.bio.sunysb.edu/morph/
Materials and Methods

Study Population

A stock of “stream-type” chinook salmon cultured at the NOAA Fisheries Research Station at Little Port Walter Alaska was used in this study. The original hatchery population was established in 1976 using gametes from 6 females and 8 males collected from the Chickamin River which is located on the mainland of Southeast Alaska (see Hard et al. 1985). The majority of fish in this stock of chinook salmon mature at age 5 although some return at age 6 and a few males return at age 4. In 1996, approximately 4 chinook salmon generations after the original hatchery stock was established, gametes were collected from 5 females and 11 males captured in the same area of the Chickamin River. A pure “wild” line was established with the gametes from 5 wild males and 5 wild females and a hybrid line was established with gametes from hatchery females, gametes from the same 5 wild males used to establish the “wild” line, and gametes from 6 additional wild males. All lines of chinook salmon released from Little Port Walter are marked with group specific coded wire tags, which are decoded before spawning the next generation.

In 2002, adult salmon progeny from the hatchery, “wild”, and hybrid lines returned to the hatchery and were spawned to continue the hatchery and wild derived lines and produce second generation hybrid crosses with the hatchery line. All lines were raised at Little Port Walter using standard hatchery techniques in which juveniles spend over one year in culture, smolts are released to sea, and all freshwater life stages from
spawning onward are artificially controlled: environmental rearing differences between lines were thus minimized.

In conjunction with another study, parentage analysis was performed on all “wild” adult spawners in order to ensure that inbreeding did not occur; this allowed us to determine the relatedness of all the wild families under the assumption that the original 8 adults collected in 1996 were not related. All wild families tested in this study were related, ranging from cousins to double cousins to half-sibs (Figure 1). Although parentage analysis was not performed for hybrid fish, the small number of wild adults used in 1996 indicates that second generation hybrid families tested may be inbred and have an unknown degree of relationship with each other, ranging from unrelated to half cousins to double half cousins. In addition, second generation hatchery wild hybrids tested have an unknown degree of relationship with the wild derived families tested, ranging from unrelated to half cousin to double half cousin. Finally, the small number of founders used for the establishment of the hatchery population in 1976 indicates that founder effect and genetic drift will have significant influence over the genetic dynamics of this population.

Five individual families from the hatchery line, five from the wild line, and five from the second generation hybrid line were tested. Within each line, two families shared a sire (half-sibs) and relatedness beyond this was not determined except as detailed above. Individual fish were randomly selected shortly after ponding; an entire family was placed into a 10 liter tray and a small dip-net was used to capture 2 or 3 fish at a time without conscious selection until a total of 60 fish from each family was attained. Each
of the 15 families was separately raised in micro vertical raceways (see Heintz and Joyce 1992). Fish were fed commercial fish food several times daily according to the manufacturer’s instructions.

Morphometric Analyses

Fish were anesthetized with MS-222 (Tricaine methansulfonate) in order to obtain fork lengths, weights, and digital photographs of their left sides. All measurements and photographs were taken on the 13th and 14th of August 2003. Ten individuals were randomly chosen from each of the 15 families by dip-netting from the micro vertical raceways without conscious selection, resulting in a sample size of 50 from each of the three lines. 13 landmarks closely associated with skeletal features and reliably identified on the photographs were digitized using the program TpsDig© (Rohlf 1998; Figure 1).

Analysis of variance (ANOVA) was performed on the standard measurements of fork length, weight, and condition factor (100,000*length/weight³) according to the model:

\[ Y_{ijk} = L_t + F_{ij} + e_{ijk} \]  

where \( Y_{ijk} \) is the length weight or condition factor, \( L_t \) is the theoretical population mean, \( L_t \) is the effect of line of origin, \( F_{ij} \) is the effect of family nested within line of origin, and \( e_{ijk} \) is the random error.

Thin plate spline analysis methods generally followed the same protocol as Hard et al. (2000). The consensus configuration was computed using the program TpsRelw© (Rohlf 2001), which employs the algorithms described by Rohlf and Slice (1990) and
Bookstein (1996). Centroid size, corresponding to the sum of squared distances between each landmark and the centroid for a specimen, was used as a measure of multivariate size. Thin-plate splines of the aligned landmark constellations were constructed with TpsRelw in order to visualize shape deformation on different geometric scales (principal warps; Rohlf and Slice 1990). This technique allows the geometric form of each specimen to be represented on Thompson (1917)-style transformation grids for improved visualization of geometric shape differences between individuals. The consensus configuration provides the template from which deviations characterize the magnitude and direction of these differences. Specifics of this method are given in Bookstein (1991) and Rohlf (1993).

Relative Warp Analysis and Evaluation of Group and Size Effects

Relative warps were computed from the landmark data to summarize the variation in shape among fish. Two types of shape variation are defined by this method: affine (uniform) and nonaffine (non-uniform). Affine variation is due to changes in shape by the same ratio in orthogonal directions while nonaffine is other i.e., non-proportional, shape variation (characteristically reflected in local deformations of a spline). The relative warps analysis performed by TpsRelw is a principal components analysis of a covariance matrix of partial warps scores computed from the landmark coordinates. The relative warps are eigenvectors. Representing patterns of shape change, these warps are interpreted through the loadings of the principal warps on them.

Multivariate analysis of variance (MANOVA) was performed on the partial warp scores between lines (hatchery-wild derived, hatchery-hybrid, and wild derived-hybrid)
according to Model (1), where $Y_{ijk}$ is the vector of partial warp scores. ANOVA was then performed on the 22 individual partial warp scores among lines according to Model (1), where $Y_{ijk}$ is the univariate partial warp score, and multiple comparisons were made with the Tukey method. ANOVA was also performed on the 22 individual partial warp scores within each line according to the following model:

$$Y_{ij} = \mu + F_i + e_{ij}$$ (2)

where $Y_{ij}$ is the individual partial warp score, $\mu$ is the theoretical population mean, $F_i$ is the effect of family, and $e_{ij}$ is the random error.

Canonical discriminate analysis (CDA) was applied to the warp matrix in order to determine the degree of morphometric differentiation first among all lines and then between the hatchery and wild derived lines. In order to characterize the effects of size on shape, all warp scores were then regressed on centroid size using multivariate regression and the fit of the data to the regression model was tested with a generalization of Goodall's (1991) F-test for group differences.

Results

Standard Measurements

The mean length, weight, and condition factor of all fish tested were 82.5mm ± 5.74, 7.34g ± 1.72, and 1.28 ± 0.09, respectively. There were no significant differences between the wild derived fish and hatchery or hybrid fish in any of these variables. Hatchery and hybrid fish differed significantly in length ($F=4.36$, $df=2,135$, $p=0.015$) and weight ($F=4.23$, $df=2,135$, $p=0.017$) but not condition factor (Table 1). Family had a
significant effect on length (F=2.75, df=12,135, p=0.002), weight (F=3.71, df=12,135, p=<0.001), and condition factor (F=6.60, df=12,135, p=<0.001).

Consensus Configuration and Relative Warp Analysis

Squared coordinate distances yielded by the linearized Procrustes estimate (Bookstein 1996) of the uniform shape component were \( x^2 = 0.94 \) and \( y^2 = 0.06 \) indicating an average aspect ratio (long axis:short axis) of 3.80 for the entire juvenile chinook salmon sample. Exploratory data analysis of the partial warp scores demonstrated no major departures from normality.

Uniform shape variation visualized as deformations of the consensus configuration corresponding to variation among individual fish in partial warps indicated greater horizontal than vertical variation. The nonaffine component of shape variation revealed shape deformations across the whole form in all 22 principal warps. Deformations included relative size of the hind and fore body, a twisting of the body, and relative size and shape of the caudal peduncle.

The ordination of nonaffine morphometric variation among the 150 fish along the first two relative warps is shown in Figure 2. Loadings on the first relative warp were highest for the vertical component of the largest principal warp (10y) followed by the horizontal component of uniform variation and the horizontal components of principal warps 7, 10, and 1. Loadings on the second relative warp were highest for the horizontal component of principal warps 10, 5, and 4, as well as the x and y components of uniform variation.
Deformations of the consensus configuration corresponding to different pairs of relative warps were visualized by TpsRelw® (Rohlf 2001) on grid plots. The plot of relative warps 1 and 2 revealed deformations associated with a bowing along the x axis, the relative size and shape of the head and fore body, and the relative size and shape of the caudal peduncle (Figure 3). Relative warps 2 and 3 were associated with deformations in the mid body depth, shape of the head, and shape of the caudal peduncle. These 3 warps accounted for 55.74% of the variation in shape.

Analyses of Group and Size Effects

MANOVAs of the effect of line on variation in partial warp scores indicated highly significant morphometric differences among all 3 lines (Table 2). Univariate analysis revealed the greatest number of differences between the hatchery and wild derived lines (11 of 22 partial warp scores differed significantly) followed by the hatchery and hybrid lines (8 of 22 partial warp scores differed significantly) and lastly, the wild derived and hybrid lines (3 of 22 partial warp scores differed significantly); family was a significant factor in 21 of 22 partial warp scores (Table 3). ANOVAs of within line partial warp scores according to Model (2) revealed significant differences between families within all lines; hatchery families differed significantly in 16 of 22 partial warp scores, hybrid families differed significantly in 16 of 22 partial warp scores, and wild derived families differed significantly in 8 of 22 partial warp scores.

Canonical discrimination analysis (CDA) also revealed significant differences among all lines (Table 4). Cross-validation of the CDA indicated that 82% of fish were correctly classified as hatchery, 66% were correctly classified as hybrid, and 58% were
correctly classified as wild (Table 5, see Figure 4). When hybrid fish were removed from the mix, 88% of fish were correctly classified as hatchery and 90% were correctly classified as wild (Table 6, see Figure 5).

The program TpsRegr\textsuperscript{©} (Rohlf 2000) was used to visualize difference in shapes between the hatchery and wild lines of fish. Shape differences between the lines were subtle. Hatchery fish were more compressed in body depth, had a narrower head, shorter maxilla, and a longer and narrower caudal peduncle than wild fish (Figure 6).

Multivariate regression of the partial warp scores on centroid size (Wilks lambda 0.416, p < 0.00001) showed that 11 of the 22 partial regression coefficients were significant at the 5% level. Goodall's test indicated a significant fit to the model (F\textsubscript{22,3256} = 7.7258, p < 0.0001), but the model explained less than 5% of the sum of the squared Procrustes residual distances. An increase in size as measured by centroid size was associated with a more robust body form (Figure 7).

Discussion

The results of this study indicate significant morphometric differences between juveniles of a hatchery stock of chinook salmon and juveniles derived from their wild founding stock. Differences observed were that hatchery fish were more dorso-ventrally compressed, had a narrower head, shorter maxillae, and a longer and narrower caudal peduncle than wild fish. These differences are consistent with previous studies on juvenile coho salmon in which the wild salmon had larger head dimensions and greater body depths than did hatchery salmon (Taylor 1986, Swain et al. 1991). Taylor's (1986) study was conducted on wild fish that were raised in the wild and hatchery fish (produced
from wild broodstock) that were raised in the hatchery. He concluded that the observed morphological differences reflected environmental differences. Swain et al. (1991) tested for a genetic component of morphological differences between hatchery and wild fish by comparing hatchery fish raised in the hatchery, wild fish raised in the hatchery, and wild fish raised in the wild. They observed that the most significant differences were found between the wild fish raised in the wild and the two types of fish raised in the hatchery. Some differences also existed between the wild fish raised in the hatchery and the hatchery fish raised in the hatchery. These results led the authors to conclude that while some evidence for genetic divergence exists, most observed differences were related to rearing environment.

In this study all three lines of juvenile chinook salmon tested (a hatchery line, a wild line derived from the same stock that originally founded the hatchery stock, and a second generation hybrid cross between the hatchery and wild stocks) were produced from parents raised in the hatchery environment and were in turn raised in the hatchery environment. This suggests that the differences observed between lines are genetic in origin and are a result of divergence of the hatchery stock from the founding wild stock. Furthermore, second generation hybrids between the two lines were morphologically intermediate to but differed significantly from both the hatchery and wild lines and they appeared to be more similar to the wild line. This also suggests a genetic component to the differences in morphology between hatchery and wild derived fish.

The demonstration of a genetic divergence in juvenile morphology between a hatchery stock and wild juvenile chinook salmon is not surprising because variation of
juvenile morphometry of hatchery chinook salmon has been shown to have a substantial genetic component (Hard et al. 1999). There are likely several underlying sources of the morphological divergence observed in this study. Firstly, because there were so few founders of the original hatchery stock in 1976 (6 female and 8 males) and these founders were collected from one area of the Chickamin River at one time, founder effect and subsequent genetic drift has likely played a role. It is probable that the original founders did not fully represent the genetic variation in the wild population, and although the number of breeders in the hatchery population has been high in subsequent generations, it is likely that inbreeding occurred. Because the number of adults sampled in 1996 was also small, 5 females and 11 males, these fish again most likely did not represent the genetic variation present in the wild population. Although the wild derived families tested in this study were not inbred, they were related, ranging from half-sibs to cousins and double cousins. The genetic structure stemming from the original founders of the hatchery population and the close family relationships of the wild derived fish tested may explain the divergence observed between these lines of fish. Of note, the family effect on morphology detected in this study was at least as significant as the effect of line of origin.

Since morphology is one of the characters expected to be subject to different selection pressures between hatchery and wild environments (Fleming and Gross 1989), another possibility is that hatchery fish have experienced domestication as a result of artificial culture. Functionally speaking, a deeper robust body such as that observed in the wild fish appears optimal for burst swimming performance while a more streamlined fusiform body such as that observed in the hatchery fish is adapted to prolonged
swimming performance (Taylor and McPhail 1985b). Hatchery culture may select
towards a more fusiform body shape because hatchery fish are typically cultured in
vessels with constant flows and released as smolts into the sea; any selective pressure
exerted by the natural freshwater rearing environment, such as predation pressure and
variable flow regimes, are absent. This may result in no selective advantage of the deep
body shape advantageous for the burst swimming performance important in predator
avoidance and food capture, and a possible advantage of the fusiform body shape more
efficient for prolonged swimming performance. It is possible that the high growth rate
experienced in hatcheries is an environmental cue for a switch in morphological
development (Martin 1949). If the fastest growing fish have the most streamlined bodies
or if the most streamlined fish are the fastest growing, there may be a selective advantage
for the streamlined body shape; once salmonids have smolted, the largest fish may have
Additionally, artificial spawning in the hatchery environment removes the selective
pressure for secondary sexual characteristics important for successful spawning in nature
and this may have an influence on morphology of subsequent generations.

The morphological differences observed between hatchery and wild derived fish
in this study were subtle but detectable. These differences were in the direction predicted
by evolutionary theory (Fleming and Gross 1989) and appear to be genetic in nature. This
is consistent with the idea that hatchery culture during the short freshwater rearing phase
of chinook salmon and subsequent artificial mating of adults without conscious selection
can resulted in a genetic divergence away from the body form that has evolved in wild
juvenile chinook salmon. Founder effects and genetic drift undoubtedly played a role in the morphological differences observed between these lines. The fact that hybrids of the wild and hatchery fish exhibited intermediate morphology tending towards wild morphology suggests that the morphology of the wild fish exhibits some directional dominance or effects of maternal environment. If so, the genetic effects of artificial culture on the morphology of juvenile chinook salmon might be reversed through natural selection.

Acknowledgments

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Figure 2.1. Landmarks analyzed; photo of juvenile chinook salmon showing the 13 digitized landmarks used in the morphometric analysis.
Figure 2.2. Ordination on relative warps 1 and 2 of the 150 juvenile chinook salmon by line. The two relative warps explained 48.3% of the total variance in shape in the sample.
Figure 2.3. Deformations associated with relative warps 1 and 2, and the consensus configuration shown represented on thin-plate splines. +, positive warp scores; -, negative warp scores.
Figure 2.4. Ordination along two canonical discriminant functions of hatchery, hybrid, and wild juveniles. The first discriminant function accounted for 84.5% of the morphometric variation in these lines of fish; the canonical correlations for the two functions were 0.817 and 0.518, respectively.
Figure 2.5. Ordination along one canonical discriminant function of hatchery and wild juveniles. The discriminant function accounted for 100% of the morphometric variation in these two lines of fish; the canonical correlation for the function was 0.876.
Figure 2.6. Deformations associated with fish line; grids depict shape differences (at 3x magnification) between juvenile chinook salmon of hatchery and wild lines. Deformation grids were generated by regressing partial warp scores against dummy variables representing fish line using the software TpsRegr (© Rohlf 1998)
Figure 2.7. Deformations associated with fish size; grids depict shape differences associated with size of juvenile chinook salmon. Deformation grids were generated by regressing partial warp scores against centroid size using the software TpsRegr (© Rohlf 1998)
**Table 2.1.** Mean lengths, weights, and condition factors of the three lines of fish tested. Differing letters indicate significant differences between lines. See text for associated statistics.

<table>
<thead>
<tr>
<th></th>
<th>Length (mm)</th>
<th>Weight (g)</th>
<th>Condition Factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery</td>
<td>81.04 ±5.21\textsuperscript{a}</td>
<td>6.88 ±1.47\textsuperscript{c}</td>
<td>1.27 ±0.08\textsuperscript{e}</td>
</tr>
<tr>
<td>Hybrid</td>
<td>84.14 ±5.92\textsuperscript{b}</td>
<td>7.76 ±1.76\textsuperscript{d}</td>
<td>1.28 ±0.08\textsuperscript{e}</td>
</tr>
<tr>
<td>Wild</td>
<td>82.32 ±5.75\textsuperscript{ab}</td>
<td>7.37 ±1.82\textsuperscript{cd}</td>
<td>1.29 ±0.10\textsuperscript{e}</td>
</tr>
</tbody>
</table>
Table 2.2. Results of MANOVAs on the vector of partial warp scores between lines.

<table>
<thead>
<tr>
<th></th>
<th>approx. F</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery-Hybrid</td>
<td>11.53</td>
<td>22,77</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Hatchery-Wild derived</td>
<td>7.27</td>
<td>22,77</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Hybrid-Wild derived</td>
<td>2.62</td>
<td>22,77</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Table 2.3. Results of ANOVAs under Model (1) on individual partial warp scores between lines. Only partial warps that differed significantly are listed, in order of decreasing significance.

<table>
<thead>
<tr>
<th>Partial Warps</th>
<th>df</th>
<th>p-value range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery-Hybrid</td>
<td>5x, 1x, UniX, 8x, 6x, UniY, 9x, 7x</td>
<td>2,135</td>
</tr>
<tr>
<td>Hatchery-Wild derived</td>
<td>5x, 1x, UniX, 9y, 8x, UniY, 4x, 9x, 2y, 10y, 4y</td>
<td>2,135</td>
</tr>
<tr>
<td>Hybrid-Wild derived</td>
<td>1x, 9y, 6x</td>
<td>2,135</td>
</tr>
<tr>
<td>Significant Family Effect</td>
<td>2x, 7x, UniX, 9y, 7y, 6y, 5x, 2y, 3y, 9x, 6x, UniY, 8x, 4y, 10y, 1y, 1x, 8y, 5y, 4x, 10x</td>
<td>12,135</td>
</tr>
</tbody>
</table>
Table 2.4. Hotelling’s T Squared for differences in means between lines of fish as generated by canonical discriminant analysis.

<table>
<thead>
<tr>
<th></th>
<th>F</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery-Hybrid</td>
<td>6.60</td>
<td>22,126</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Hatchery-Wild derived</td>
<td>10.92</td>
<td>22,126</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Hybrid-Wild derived</td>
<td>2.82</td>
<td>22,126</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Table 2.5. Cross-validation table for three lines; jackknifed classification matrix generated from canonical discriminant analysis of partial warp scores of hatchery, hybrid, and wild fish lines.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Hatchery</th>
<th>Hybrid</th>
<th>Wild</th>
<th>Error</th>
<th>Posterior Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery</td>
<td>50</td>
<td>41</td>
<td>8</td>
<td>1</td>
<td>0.18</td>
<td>0.12</td>
</tr>
<tr>
<td>Hybrid</td>
<td>50</td>
<td>5</td>
<td>33</td>
<td>12</td>
<td>0.34</td>
<td>0.15</td>
</tr>
<tr>
<td>Wild</td>
<td>50</td>
<td>3</td>
<td>18</td>
<td>29</td>
<td>0.42</td>
<td>0.33</td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.31</td>
<td>0.20</td>
</tr>
</tbody>
</table>
Table 2.6. Cross-validation table for two lines; jackknifed classification matrix generated from canonical discriminant analysis of partial warp scores of hatchery and wild fish lines only.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Hatchery</th>
<th>Wild</th>
<th>Error</th>
<th>Posterior Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery</td>
<td>50</td>
<td>44</td>
<td>6</td>
<td>0.12</td>
<td>0.049</td>
</tr>
<tr>
<td>Wild</td>
<td>50</td>
<td>5</td>
<td>45</td>
<td>0.10</td>
<td>0.034</td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td></td>
<td></td>
<td>0.11</td>
<td>0.042</td>
</tr>
</tbody>
</table>
References


General Conclusion

Behavior and morphology differed significantly between juveniles of a hatchery stock of chinook salmon and juveniles derived from their wild founding stock, and these differences appeared to be genetic rather than environmental, in origin. While the demonstration of these differences is consistent with the idea that domestication has occurred in these fish, several other factors are likely influencing the observed divergence between these populations of fish.

The original hatchery stock was established from just 6 females and 8 males collected at one time from one area on the Chickamin River, indicating that a founder effect may influence the genetic dynamics of the hatchery population. It is likely that the original broodstock was representative of just a small portion of the genetic variation contained in the wild population; furthermore, although the number of breeders in the hatchery population has been high in subsequent generations, it is likely that inbreeding occurred. Because random genetic drift has most certainly occurred in the hatchery population and because the original broodstock may not have been representative of the wild population, genetic differences would almost certainly be expected between the hatchery population and a population newly derived from the wild founding population. Further complicating matters, the 1996 sampling again included very few adults, 5 females and 11 males, collected at one time from one area of the Chickamin River. Again, these fish most likely represent a small portion of the genetic variation found in the wild. Genetic and phenotypic differences would be expected between fish derived from this group of wild fish and the hatchery population established in 1976. Finally,
because of logistical constraints, only five families from each line (hatchery, hybrid, and wild derived) were tested.

Although morphology was shown to vary significantly between families, agonistic behavior was not. This may mean that the variance in agonistic behavior found in one family or several families could be representative of the greater population while the variance in morphology found in one family or several families does not necessarily represent the greater population.

The increased aggressiveness and the changes in body morphology observed in the hatchery fish were both consistent with previous studies on hatchery and wild salmonids (Moyle 1969, Taylor 1986, Swain and Riddell 1990, Mesa 1991, Swain et al. 1991). This is consistent with the idea that directional and selected changes are occurring in hatchery salmonids beyond random genetic drift.

While founder effects, genetic drift, and a small number of families sampled most certainly have had an affect on the genetic make up of the populations and individuals tested in this study, and the observations reported, the results of this study are still consistent with the changes expected with domestication. Future studies in this area should endeavor to study hatchery populations less profoundly impacted by founder effects and sample from greater numbers of families. Meanwhile, cautious interpretation of these results suggests that hatchery technologies continue to be evaluated and improved with the goal of minimizing the negative effects of culturing.
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