Evidence for morphometric differentiation of wild and captively reared adult coho salmon: a geometric analysis

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Synopsis

As part of a comprehensive genetic evaluation of reproduction in naturally spawning coho salmon, *Oncorhynchus kisutch*, we examined morphometric variation in captively reared and wild adults from Hood Canal, Washington (U.S.A.) for evidence of differentiation between these groups. We collected captively reared fish as parr from two stocks and reared to adulthood at a freshwater hatchery, maturing in 1995 and 1996; we sampled closely size-matched wild fish as they returned to a neighboring stream in both years. Multivariate analysis of shape variation by Procrustes coordinates, visualized by thin-plate splines, indicated that the captively reared adults were differentiated from the wild fish by sharply reduced sexual dimorphism as well as smaller heads and less hooked snouts, increased trunk depth, larger caudal peduncles, shorter dorsal fins, larger hindbodies and a reduction in body streamlining. The differences between the captively reared and wild fish were similar to but more pronounced than some differences previously reported between hatchery and wild coho salmon. The magnitude and pattern of differences suggested that at least some of them were environmentally induced. Shape variation showed an allometric relationship with variation in body (measured as centroid) size. Morphometric variation was a poor correlate of most spawning behaviors. Nevertheless, our results suggest that the morphometric consequences of captive rearing for mate selection and reproductive activity of spawning fish may limit its effectiveness as a restorative tool.

Introduction

Captive rearing of anadromous salmonids involves protective culture of fish without artificial spawning; it is a method that consists of collecting gametes or juveniles, culturing these fish to adulthood and releasing them upon maturation into streams to spawn naturally (Berejikian et al. 1997). Consequently, captively reared (hereafter, captive) fish experience environments during development and maturation that differ markedly from those encountered by wild fish or by hatchery fish released as juveniles to the wild. Nevertheless, captive rearing holds promise as a method for increasing the abundance of adults available for spawning in natural habitats because it limits the opportunity for genetic divergence from wild fish by allowing sexual selection and natural selection during early development to occur in the wild.[1]

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[1] Hard, J.J., R.P. Jones, M.R. Delarm & R.S. Waples. 1992. Pacific salmon and artificial propagation under the Endangered

However, captive rearing is largely untested as a recovery tool, and its genetic and ecological risks are not well understood. Moreover, although changes in adult appearance and behavior appear to be prominent consequences of domestication in salmon (Fleming & Gross 1992, 1993, 1994, Fleming et al. 1996, Berejikian et al. 1997, Fleming & Einum 1997), considerable uncertainty remains regarding the influence of domestication on morphometry, sexual selection and reproductive success. Variation in body size and shape may profoundly influence mating patterns, spawning behavior and productivity of captively reared individuals in the wild and, consequently, the effectiveness of captive rearing as a restorative tool.

Morphometric variation in adult male and female salmon, including coho salmon, *Oncorhynchus kisutch*, has been described in several studies (Beacham 1985, Beacham & Murray 1985, Beacham & Withler 1985, Beacham et al. 1988, Fleming & Gross 1989, 1994, Lund et al. 1989, van den Berghe & Gross 1989, Fleming et al. 1994, 1996, Kinnison et al. 1998). Most of these have analyzed conventional body measurements. These studies indicate that morphometry (1) can be highly variable among and within conspecific populations, (2) is often correlated with geographic and habitat variation and (3) often appears to have a genetic component, based on differences among groups in a common environment. Conspecific comparisons of cultured and wild salmon have generally found that cultured fish exhibit less fusiform shape, larger trunks, shorter dorsal humps, smaller heads and kypes and shorter fins than wild fish of similar size.

In this paper we use a geometric method based on analysis of body landmarks to characterize morphometric variation in wild and captive adult coho salmon. Compared with other approaches, this method improves both the function of describing and archiving body size and shape and the ability to discriminate among biologically relevant groups. The method's hallmark is analysis of the geometry of the entire landmark set, rather than subsets of linear distances between landmarks (Rohlf 1990, Rohlf & Marcus 1993). The method extracts features of pure geometric shape variation from the same raw

information (landmark data) used in multivariate methods such as principal components analysis of truss elements. Both methods are improvements upon univariate measurements in that they provide more systematic coverage of the entire form, permitting its shape to be archived easily and improving standardization (Strauss & Bookstein 1982), but geometric methods further permit characterization of shape variation across a wide range of spatial scales.

In a previous paper, we showed that captive coho salmon spawned successfully with 'wild' fish (defined as naturally rearing progeny of naturally spawned parents) in an experimental stream and demonstrated the range of reproductive behaviors displayed by closely size-matched wild fish (Berejikian et al. 1997). Nevertheless, several patterns were apparent: captive males showed lower dominance status than wild males, both captive and wild females spawned less frequently with captive males, and captive females were less active reproductively than wild females. Our objective in this paper is to describe morphometric variation in these groups and examine its relationship to variation in reproductive behavior. By relating the morphometric data in this paper to our previous study we also examine to what extent, at the group level, adult morphometry and reproductive behavior are correlated. In a subsequent paper we shall examine the relationship between adult morphometry and reproductive behavior of these fish and determine the consequences of this relationship for reproductive success.

Materials and methods

Sample collection

We analyzed morphometric variation in captively reared and putatively 'wild' coho salmon from two broods maturing in 1995 and 1996. Captive and wild fish were collected from three neighboring (within a 10-km radius) stocks in northeastern Hood Canal, Washington in October and November 1995 and from two of these stocks in 1996. Details of the 1995 collections and the rearing procedures appear in Berejikian et al. (1997); captive fish were reared outdoors in freshwater from the parr interval to adulthood in circular tanks at low densities on a conventional hatchery diet. The data considered in our analysis include 19 captively reared adults (10 females and 9 males) collected as wild juveniles from Stavis Creek in 1992 and maturing in 1995, 19 wild adults (10 females

Species Act. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC 2. 56 pp.

Flagg, T.A. & C.V.W. Mahnken. 1995. An assessment of the status of captive broodstock technology for Pacific salmon. Final Report to the Bonneville Power Administration (Project No. 93-56), P.O. Box 3621, Portland. 225 pp.

and 9 males) collected from Big Beef Creek in 1995, and 27 captively reared adults (sexes not identified) collected as wild juveniles from Big Anderson Creek in 1992 and maturing in 1995. Repeated attempts to collect sufficient wild adults from Stavis Creek in 1995 with a weir and by seine were unsuccessful; therefore, the Big Beef Creek fish were used as surrogate wild fish in this experiment.

We analyzed scale patterns of each of the adults collected from Big Beef Creek to confirm that all were progeny of naturally spawning parents. Berejikian et al. (1997) argued that the close proximity of Big Beef Creek, Stavis Creek, and Big Anderson Creek and recent straying of hatchery fish into these northeastern Hood Canal streams is likely to have limited genetic differences between these populations, and they used this argument to support the use of Big Beef Creek wild adults as a surrogate for wild Stavis Creek adults in their study. The extent to which naturally spawning hatchery fish contributed to the Big Beef Creek fish in our collection is not known, but the possibility of some contribution led us to surmise that any morphometric differences we observed between the Big Beef Creek and the captive adults are likely to underestimate the differentiation of wild and captive fish.

We photographed the captively reared and wild adults under anesthesia and based our analyses on the digital images. We also photographed adults from Big Anderson Creek (captive) in 1995 to help assess whether morphometric differences observed between Stavis Creek (captive) and Big Beef Creek (wild) adults were the result of environmental or genetic factors. Unlike the Stavis Creek and Big Beef Creek adults, we were unable to assign sexes reliably to Big Anderson Creek adults from photographs alone, as supplemental measurements were not collected from them.

The 1996 data considered in this paper were collected from fish sampled in October and November from 48 Stavis Creek captive adults (25 females and 23 males) and 36 Big Beef Creek wild adults (17 females and 19 males). Data collection was similar to that in 1995. We were able to recover two wild males returning to Stavis Creek in 1996, and these adults were also photographed for morphometric analysis. The complete dataset over the two years included 151 adults.

Morphometric analyses

Analyses based on the truss have been applied to the analysis of morphological variation in juvenile salmon

(Winans & Nishioka 1987, Beeman et al. 1994, 1995; but see Unwin et al. 1999). An important limitation of such analyses is that they rely on the identification of axes of shape variation (e.g., principal components) that are not direct representatives of the form under study, which can make biological interpretation difficult (Rohlf et al. 1996, Yaroch 1996). This approach may be particularly limiting when shape variation involves several landmarks on small geometric scales. Moreover, Bookstein (1991) noted that the truss can only approximate variability in shape of forms that differ in size. Recently developed geometric analyses of landmark coordinates (e.g., shape coordinates, relative warps) circumvent this limitation by providing robust measures of the variation among specimens in Procrustes distance (Bookstein 1996). This feature of geometric methods permits a fuller characterization of multivariate shape variability, especially when size differences among specimens are small (Bookstein 1991, Yaroch 1996), and we apply these methods here.

The basis of our analysis of morphometric variation was a comparison of landmark data collected from digital images of the lateral view of each adult to a generalized orthogonal least-squares Procrustes mean configuration of landmarks computed from these data (the 'consensus' configuration). We photographed 151 adults while they were anesthetized for tagging and collection of information on sex, size, age and scale patterns (Berejikian et al. 1997). We identified 13 landmarks along the body form closely associated with skeletal features (Figure 1); we used relative warp analysis (Bookstein 1991) and interpolating functions known as thin-plate splines (Bookstein 1989) to characterize variation in the constellation of landmarks digitized from the images of each fish. We digitized the landmarks from the photographs with the program TPSDIG;[2] from the landmark coordinates we computed the consensus configuration using the program TPSRELW,[3] which implements the

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[2] Rohlf, F.J. 1996. TPSDIG. Program for digitizing images for analysis by thin-plate splines [Windows], version 1.08. Department of Ecology & Evolution, State University of New York, Stony Brook 11794-5245 (available by anonymous ftp from http://life.bio.sunysb.edu/morph/morph.html).

[3] Rohlf, F.J. 1997. TPSRELW. Program for analyzing landmark data with thin-plate splines using relative warps [Windows], version 1.14. Department of Ecology & Evolution, State University of New York, Stony Brook 11794-5245 (available by anonymous ftp from http://life.bio.sunysb.edu/morph/morph.html).
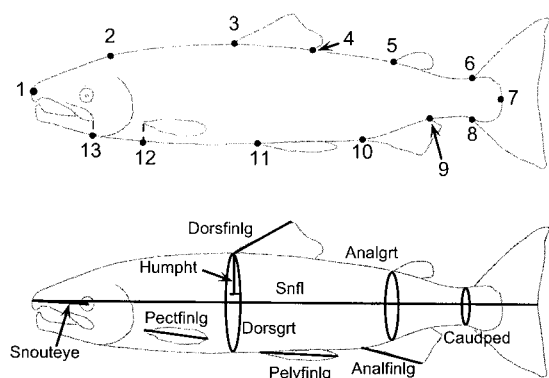
Figure 1. Locations of the 13 landmarks used to characterize morphometric variation with thin-plate splines (upper panel) and the 11 supplemental morphometric characters measured on adult coho salmon.

algorithms described by Rohlf & Slice (1990) and Bookstein (1996).

All digitizing was performed by one of us (JJH). As in a previous analysis of landmark data from juvenile chinook salmon (Hard et al. 1999), error estimated from replicate measurements taken from the same images was negligible. We used centroid size, equivalent to the sum of squared distances between each landmark and the centroid for a specimen, as a measure of multivariate size. With TPSRELW we constructed thin-plate splines of the aligned landmark constellations (using generalized least squares, or GLS, superimposition) to visualize shape deformation on different geometric scales (principal warps) (Rohlf & Slice 1990). The spline permits each specimen's geometric form to be archived and reconstructed readily and allows graphical representation of geometric shape differences among individuals on Thompson (1917)-style transformation grids. Deviations from the consensus configuration form the basis for characterizing the direction and magnitude of these differences. Details of the method are given by Bookstein (1991) and Rohlf (1993).

Relative warp analysis and evaluation of group and size effects

We computed relative warps from the landmark data to summarize the variation in shape among fish in as few dimensions as possible. The method permits characterization of two types of shape variation: affine (uniform), or that due to changes in shape by the same ratio in orthogonal directions, and nonaffine, or other shape variation (typically reflected in local deformations of a spline). In our analysis of the relative warps, we computed the overall variation in shape as the sum of squared Procrustes distances (Bookstein 1996) of the individual shapes from the consensus configuration. A relative warp analysis, accomplished here by TPSRELW, is a principal components analysis of a covariance matrix of partial warp scores computed from the distance data. The relative warps are eigenvectors that depict patterns of shape variation in the data; these warps can be interpreted through the loadings of the principal warps on them. We analyzed the warp matrix with multivariate analysis of variance (MANOVA) and canonical discriminant analysis (CDA) to determine the degree of morphometric differentiation between groups (stock, type, brood and sex). We characterized this differentiation by estimating the canonical discriminant functions of the warp scores, standardized by within-score variances (Rohlf et al. 1996). For each warp, we then regressed the scores on centroid size using multivariate regression. We tested the fit of the data to the regression model with a generalization of Goodall's (1991) F-test. The alignment scaling for centroid size in the multivariate regression analyses performed with TPSRELW used the $\cos(\rho)$ option.

Supplemental morphometric measurements

Previous studies have indicated that morphometric characters not associated with truss or trunk characteristics can differ between hatchery and wild salmon. We therefore measured several additional morphometric characters for captive Stavis Creek and wild Big Beef Creek coho salmon maturing in 1995 (Figure 1): body weight (to the nearest g) and snout-fork length (Snouteye), girth perpendicular to the lateral line at the anterior insertion of the dorsal fin (Dorsgrt), girth at the anterior insertion of the anal fin (Analgrt), girth at the narrowest point of the caudal peduncle (Caudped) and the lengths of the leading edges of the dorsal (Dorsfinlg), left pectoral (Pectfinlg), left pelvic (Pelvfinlg) and anal (Analfinlg) fins (all to the nearest mm). We analyzed variation among groups in these characters with factorial MANOVA, with stock, sex, brood year and their four interactions as fixed effects. Post-hoc tests for pairwise differences among groups incorporated the Bonferroni correction for multiple comparisons (Rice 1989).

Results

Consensus configuration and relative warp analysis

The linearized Procrustes estimate (Bookstein 1996) of the uniform shape component using GLS alignment to construct the consensus configuration yielded squared coordinate distances of $\sum x^2 = 0.949$ and $\sum y^2 = 0.051$, indicating an average aspect ratio (long axis:short axis) of 4.4 for the entire coho salmon sample. Plots of partial warp scores against standard normal expectations revealed no appreciable departures from normality. Levene's (1960) test for heteroscedasticity based on MANOVA of absolute values of partial warp scores indicated that variances did not differ between stocks ($F_{22,99} = 1.236$, $p = 0.236$) or sexes ($F_{22,99} = 0.805$, $p = 0.713$), although we detected greater variation between broods ($F_{22,99} = 2.025$, $p = 0.010$).

Deformations of the consensus configuration corresponding to variation among individual fish in partial warps (and therefore to shape variation on different geometric scales) indicated greater vertical than horizontal uniform shape variation. For the nonaffine component, shape deformations reflected variation across the entire form from the smallest to the largest principal warps (corresponding to partial warps 1x and 1y, and 10x and 10y, respectively). This variation included the relative size of the forebody and hindbody and a slight twisting along the fish's longitudinal axis (landmarks 3–5 and 8–11 in Figure 1), a smooth 'bowing' along the longitudinal axis of the fish, and the size of the anal fin base and the size and shape of the caudal peduncle and hypural plate (landmarks 6–10).

We used TPSRELW to analyze deformations of the consensus configuration corresponding to different pairs of relative warps. Deformations on the grid corresponding to a plot of relative warps 1 and 2 were associated with the size and shape of the head, the distance from the head to the dorsal fin, the relative size of the forebody and hindbody and the shape of the caudal region. Shape variation on relative warps 2 and 3 was associated with the depth of the midbody and a stretching/compression in the region between the dorsal and anal fins along the longitudinal axis, as well as head shape. Together these three warps accounted for 63.0% of the variation in shape.

Figure 2 depicts an ordination of nonaffine morphometric variation among the 151 fish along the first two relative warps. Loadings on the first relative warp were highest for the vertical (y) component of variation on
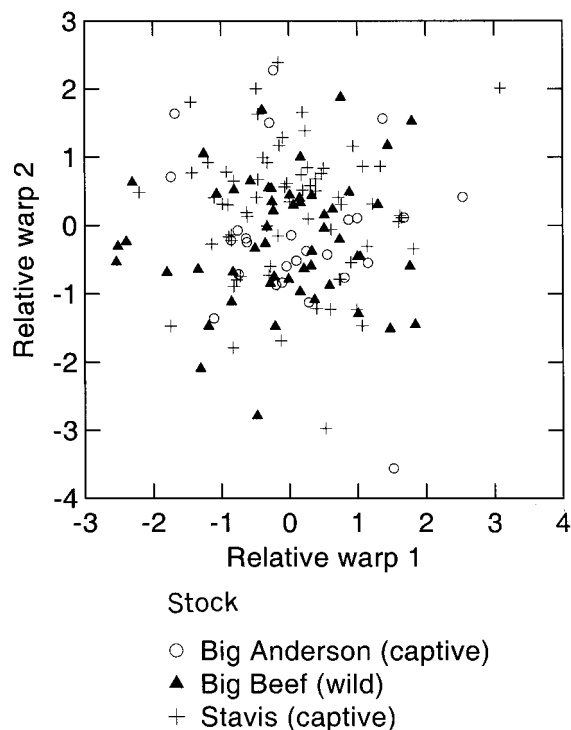

Figure 2. Scatterplot depicting ordination of the 151 adult coho salmon on relative warps 1 and 2 by stock. The ordination includes the uniform component of shape variation (i.e., partial warps are unweighted). The two relative warps explained 54.6% of the total variance in shape in the sample.

principal warps corresponding to three of the largest of the 10 nonaffine geometric scales (partial warps 7y–9y). Loadings on the second relative warp were highest for the horizontal (x) component of nonaffine variation corresponding to large geometric scales (partial warps 7x–9x) and the x component of uniform variation (warp Ux). Figure 3 shows the major deformations associated with relative warps 1 and 2. These deformations are complex, but the patterns result largely from variation in the shape of both the head and caudal peduncle region and a bowing along the longitudinal axis.

Analyses of group differences

MANOVAs of the effects of stock type, sex and brood year on variation in partial warp scores indicated highly significant morphometric differences between captive (Stavis Creek and Big Anderson Creek) and wild (Big Beef Creek) fish (Table 1). Subsequent univariate
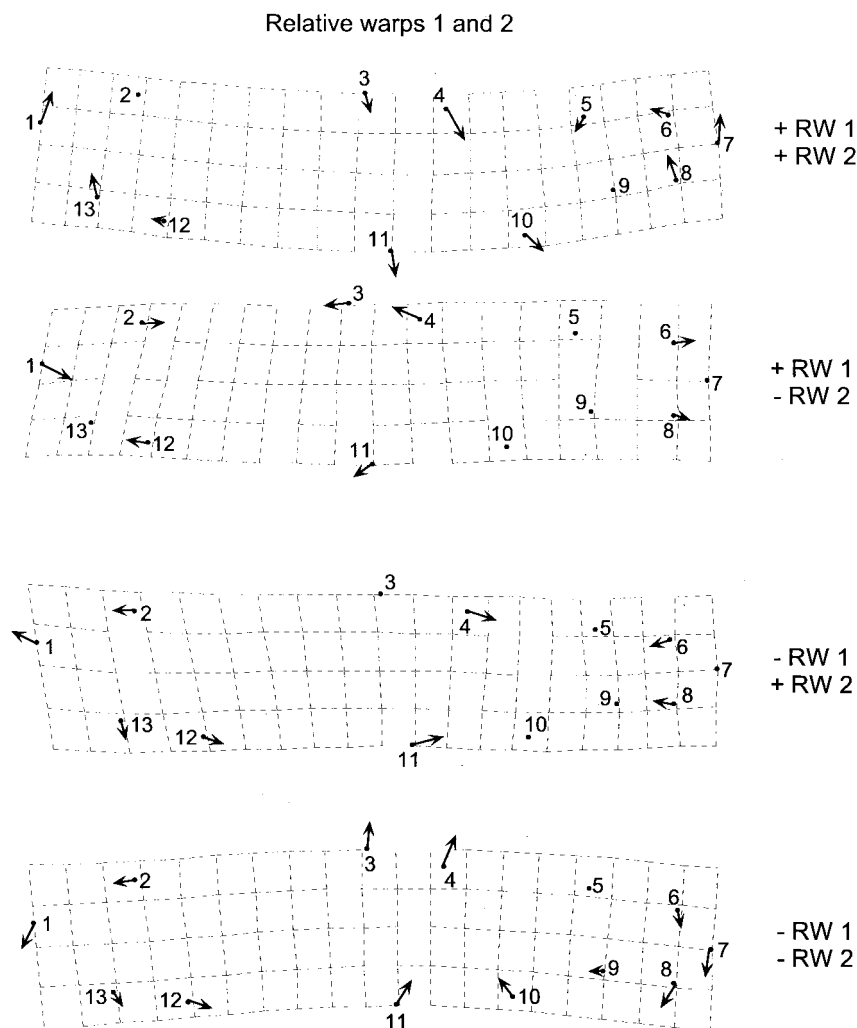
Relative warps 1 and 2

Figure 3. Thin-plate spline representation of shape deformations in adult coho salmon associated with relative warps (RW) 1 and 2. +, positive warp scores; −, negative warp scores. Arrows denote vectors for each landmark that indicate the direction and extent of shape change from the consensus configuration.

F-tests showed that different sets of partial warps were responsible for differences between types, sexes and broods. The largest differences (in decreasing order of effect) between types were due to the horizontal component of uniform variation (Ux) and both horizontal and vertical components of the two smallest principal warps (1x, 1y, and 2y) (minimum $F_{1,116} = 17.510$, p < 0.0001). The largest differences between sexes were due to variation on the same warps (minimum $F_{1,116} = 16.476$, p < 0.0001). The differences between broods were due to variation in both aspects of the uniform component and the smallest nonaffine warp (minimum

$F_{1,116} = 13.885$, p < 0.0005). Thus, most of the variation among groups of fish reflected both stretching of the consensus configuration and deformations on small geometric scales, primarily in the head and tail regions. All three two-way interactions between stock type, sex and brood were highly significant, implying substantial influences of both within- and among-year environmental effects on morphometry.

Jackknifed classification matrices generated from the CDA indicated that 85% of fish were correctly classified to Big Anderson Creek, 98% to Big Beef Creek and 87% to Stavis Creek (see Figure 4). Two Stavis

Table 1. Summary of MANOVAs of the fixed effects of stock type (C = captively reared, W = wild), sex, brood year (1992 or 1993) and their interactions on morphometric variation in adult coho salmon. Variation is measured in 22 partial warps (see text). For each test, df = 22 and 95.

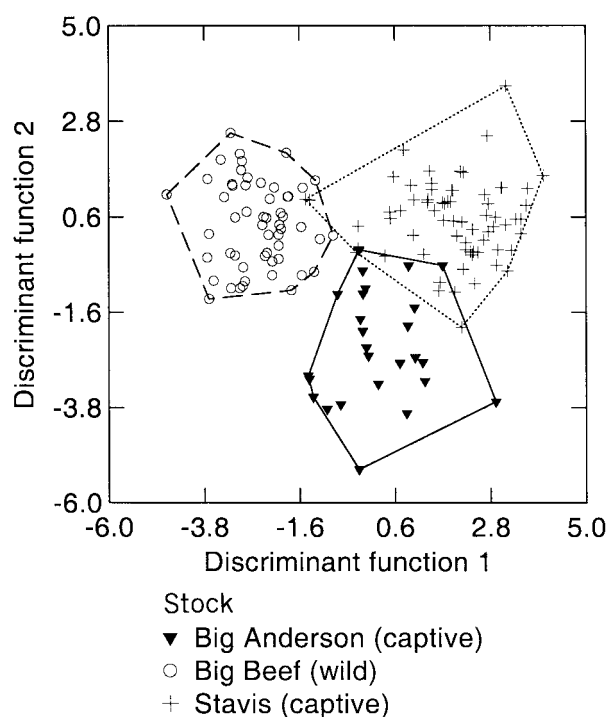| Source of variation	Wilks' Λ	F	p
Type (C or W)	0.137	27.103	< 0.0001
Sex	0.188	18.656	< 0.0001
Brood	0.239	13.773	< 0.0001
Type × sex	0.675	2.081	0.0080
Type × brood	0.451	5.265	< 0.0001
Sex × brood	0.590	3.007	0.0001
T × S × B	0.740	1.517	0.0868

Figure 4. Ordination of Stavis Creek (captive), Big Anderson Creek (captive) and Big Beef Creek (wild) adult coho salmon (sexes combined) collected in 1995 and 1996 along two canonical discriminant functions. The first discriminant function accounted for 77.3% of the morphometric variation in these groups of fish; the canonical correlations for the two functions were 0.898 and 0.742, respectively. Convex hulls outline the three groups.

Creek fish that classified with wild Big Beef Creek fish were in fact the two wild Stavis Creek males captured in 1996; accounting for this fact improved the classification rate of Stavis Creek fish to 91% and the overall classification success to 93%. Examination of

the two canonical discriminant functions separating the three stocks in Figure 4 illustrates how distinct the three stocks are morphometrically. The first canonical discriminant function accounted for 77.3% of the variation in partial warp scores, and reflected primarily uniform variation and nonaffine variation on the smallest principal warps. Nonaffine variation along this function was due to differences between wild and captive fish; more negative function values (Big Beef Creek fish) corresponded to a larger head, larger dorsal and anal fins, a thicker caudal peduncle, a deeper body, and pelvic fins located closer to the pectoral fins. The second function, which explained the remaining (22.7%) variation, reflected variation on small geometric scales corresponding to differences in head shape, pelvic fin position, and the size of the dorsal fin. Big Anderson Creek fish, which were differentiated from fish in the two other stocks along this function, tended to have smaller heads with less hooked snouts, shallower bodies, and shorter caudal peduncles.

Canonical discriminant analyses of variation in partial warp scores among the four groups that were identified by both stock and sex accomplished complete separation of these groups (approximate $F_{22,296} = 12.087$, p < 0.0001). The first two discriminant functions were associated with stock type (canonical correlation = 0.923) and sex (canonical correlation = 0.900), respectively, and together accounted for 96% of the variation (Figure 5). Jackknifed classification matrices indicated 91% correct classification of the four groups (88% for wild males, 93% for captive males, 89% for wild females and 96% for captive females).

Jackknifed classification matrices indicated 97% correct classification of types, 95% classification of sexes and 89% classification of broods. Separation of stock types, based on examination of canonical discriminant functions standardized by within-warp variances, was due primarily to variation in partial warps Ux, 1x, Uy, 1y and 2x, in decreasing order of effect. Separation of sexes was due primarily to variation in partial warps Ux, 1y, 1x, 2y and 4x; variation in partial warps 1y, Uy, Ux and 1x was responsible for most of the separation of broods. The program TPSREGR[4] provides a means to visualize the interactions of the

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[4] Rohlf, F.J. 1998. TPSREGR. Program to conduct multivariate multiple regression analysis of shape and size data [Windows], version 2.15. Department of Ecology & Evolution, State University of New York, Stony Brook 11794-5245 (available by anonymous ftp from http://life.bio.sunysb.edu/morph/morph.html).
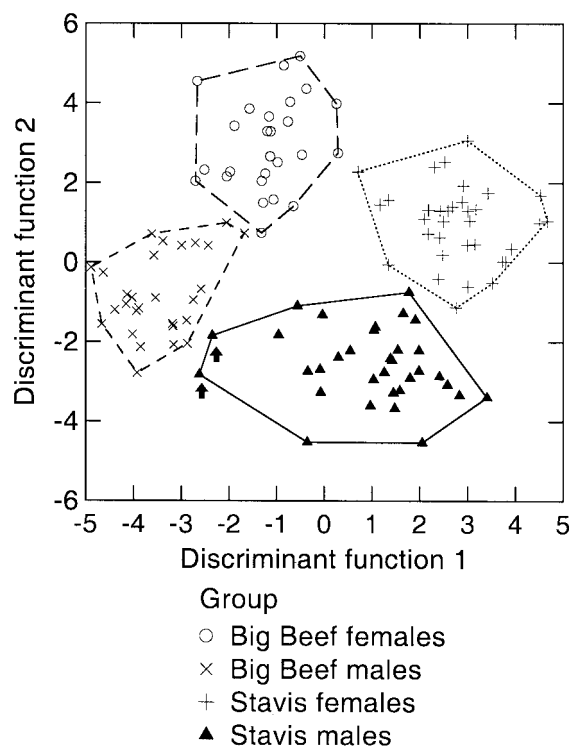
Figure 5. Scatterplot depicting ordination of male and female Stavis Creek (captive) and Big Beef Creek (wild) coho salmon along two canonical discriminant functions. These two functions accounted for 96.2% of the morphometric variation in these groups of fish; the canonical correlations for the two functions were 0.923 and 0.900, respectively. Convex hulls outline the four groups. Arrows denote the two wild Stavis Creek males collected in 1996.

partial warps on the morphometry of specimens in each group. Figure 6 shows that wild fish of both sexes were differentiated from captive fish in shape in several ways. Wild fish had longer and shallower heads, more strongly curved snouts and larger trunks, shorter bases but longer lengths of dorsal and anal fins, shorter and narrower caudal peduncles and more posteriorly placed pectoral and pelvic fins than did captive fish. The most pronounced characteristics of captive fish relative to wild fish were shorter and deeper heads, shorter and deeper trunks and proportionately larger hindbodies. Captive rearing tended to diminish much of the dimorphism apparent in wild fish, but captive males and females were still differentiated by greater dorsal hump height and head size and a more posterior positioning of pectoral and pelvic fins in males.

Relationships between shape and size

Multivariate regression of partial warp scores (including affine and nonaffine components) on centroid size (Wilks' $\Lambda_{22,128} = 0.319$, p < 0.0001) indicated that 18 of the 22 partial regression coefficients were significant at the 5% level. Goodall's test revealed a significant fit to the model ($F_{22,3278} = 15.118$, p < 0.0001), but the model explained less than 10% of the sum of squared Procrustes residual distances. Moreover, the sum over individuals of the squared Procrustes distances residual from the model relative to the total sum was large (99.0% unexplained), and Rohlf's modification of Goodall's F-test for the fit of the model indicated a poor fit to the data ($F_{22,2684} = 1.228$, p $= 0.2119$). An increase in centroid size was correlated primarily with increased head size, dorsal hump height and caudal peduncle depth, reduced dorsal and anal fin base lengths and an increased separation of pectoral and pelvic fin insertions (Figure 7).

Supplemental measurements

Supplemental body measurements showed strong sexual differences in length (p $= 0.0148$), weight (p $= 0.0053$), dorsal girth (p $= 0.0037$) and snout-eye distance (p $= 0.0112$) (Table 2). Males were larger (mean $\pm$ 1 SD) than females in snout-eye distance (1.76 ± 0.43 cm larger) and dorsal fin length (2.45 ± 0.54 cm larger), but the reverse was true for most other measurements. Significant differences between stocks existed for snout-eye distance (wild: 1.83 ± 0.38 cm vs. captive: 1.43 ± 0.43 cm; p $= 0.0002$) and dorsal fin length (wild: 2.59 ± 0.48 cm vs. captive: 2.27 ± 0.54 cm; p $= 0.0419$), and these differences held for both sexes. We observed no significant differences between captive and wild fish in anal, pectoral, or pelvic fin length ($p > 0.05$). We detected no evidence ($p > 0.10$) for a type X sex interaction in any of these characters. Multivariate test statistics indicated significant effects of type ($F_{11,19} = 2.467$, p < 0.050) and sex ($F_{11,19} = 12.208$, p < 0.0001) but not their interaction ($F_{11,19} = 1.154$, p > 0.250) on overall variation.

Discussion

This study documents substantial morphometric differences between captively reared and wild adult coho salmon. The differences we detected were expressed
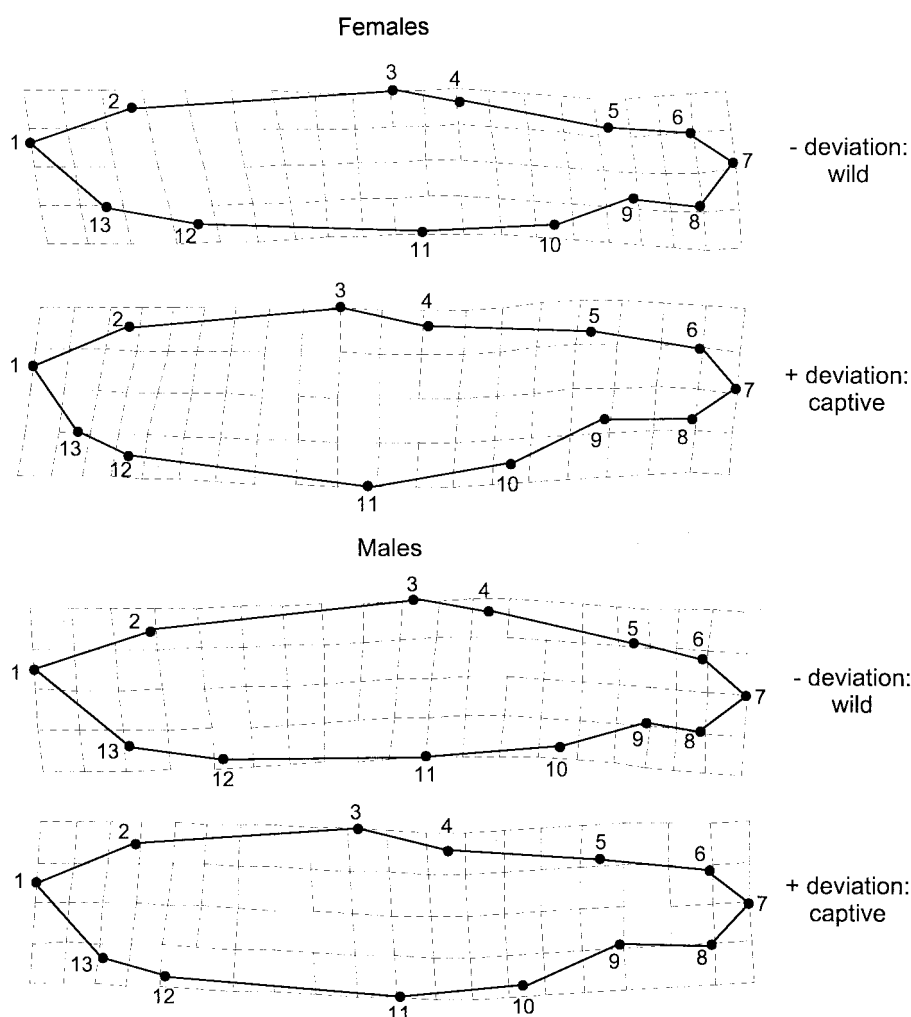
Figure 6. Thin-plate spline representation of shape deformations along canonical discriminant functions distinguishing wild from captive male and female coho salmon. The magnitude of the deformations from the consensus configuration is exaggerated two-fold to enhance the contrast.

on a wide range of geometric scales but were most pronounced on smaller scales. We detected these group differences in both sexes, and the majority of the differences between captive and wild fish were expressed on scales similar (albeit fewer and somewhat smaller) to those corresponding to sexual differentiation. Although the morphometric variation may be influenced by variation in stage of maturation, the group differences suggest that captive rearing led to sharply diminished sexual dimorphism in both the Stavis Creek and Big Anderson Creek stocks. The major morphological consequences of captive rearing appear to involve a reduction in head size and snout curvature and an increase

in head depth; increases in trunk depth, dorsal and anal fin base lengths and caudal peduncle size; reductions in lengths of the dorsal fin; a forward shifting of pelvic fin placement; and a general reduction in body streamlining. Captive rearing did not, however, eliminate sexual dimorphism. Sexual variation that remained included primarily head and dorsal hump size, snout length and paired fin position (Figure 6). Variation in body shape of fish of different size was evident: larger fish, as measured by centroid size, had relatively larger heads, dorsal humps and caudal peduncles, smaller dorsal and anal fin bases and greater separation between pectoral and anal fins than smaller fish (Figure 7).
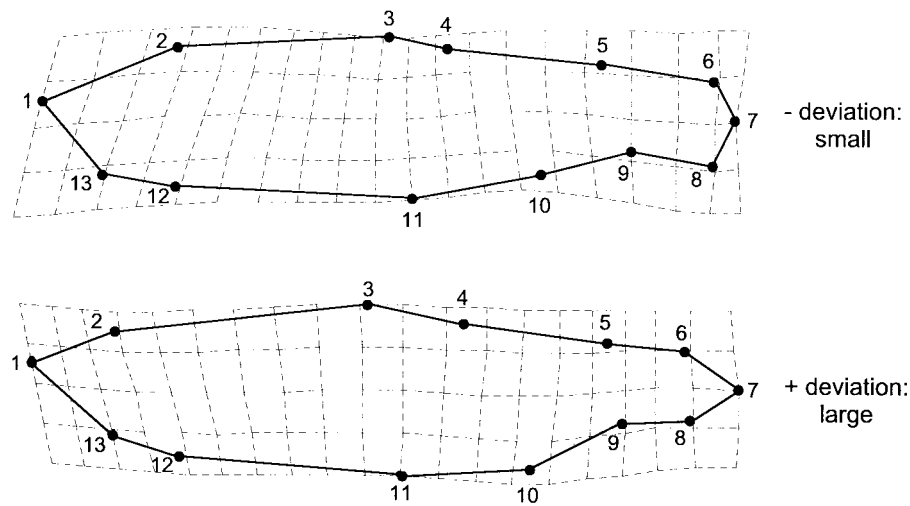
Figure 7. Thin-plate spline representation of shape deformations associated with size of adult coho salmon. The figures depict the geometric changes in fish shape with variation in centroid size. The magnitude of the deformations from the consensus configuration is shown at its actual value.

Table 2. Tests of morphometric differences between 1995-brood Stavis Creek (captively reared) and Big Beef Creek (wild) adult coho salmon. Analyses of variance for 11 supplemental morphometric measurements (see Figure 1) are summarized for the effects of the fixed factors stock and sex and their interaction. %RSS = %reduction in total sum of squares due to the factor effect; SS_{res} = residual sum of squares after all effects are accounted for. For all tests, df = 1 and 29. Bonferroni probabilities: ^{ns} = p > 0.05; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.

Trait	Stock		Sex		Stock × sex		SS_{res}
	F	%RSS	F	%RSS	F	%RSS	
Snfl	0.755^{ns}	2.02	7.425^{**}	19.34	0.453^{ns}	1.21	77.43
Wt	0.247^{ns}	0.63	9.891^{**}	25.91	0.133^{ns}	0.34	73.85
Dorsgrt	0.457^{ns}	1.12	11.146^{**}	27.34	0.169^{ns}	0.42	71.12
Analgrt	0.029^{ns}	0.09	3.026^{ns}	9.41	0.095^{ns}	0.30	90.20
Caudped	1.282^{ns}	3.84	2.591^{ns}	7.76	0.524^{ns}	1.57	86.83
Humpht	0.007^{ns}	0.04	0.084^{ns}	0.30	0.124^{ns}	0.41	99.25
Snouteye	13.345^{***}	27.79	5.264^{*}	10.96	0.403^{ns}	0.84	60.41
Dorsfinlg	6.029^{*}	16.34	0.046^{ns}	0.11	1.821^{ns}	4.94	78.61
Analfinlg	6.116^{ns}	15.66	3.783^{ns}	9.69	0.173^{ns}	0.46	74.19
Pectfinlg	3.684^{ns}	10.83	2.893^{ns}	8.12	0.029^{ns}	0.08	81.47
Pelvfinlg	3.967^{ns}	10.99	0.972^{ns}	2.70	2.133^{ns}	5.90	80.41

The morphometric characteristics of captive fish were qualitatively similar to those that have been observed in adult salmon released from hatcheries as juveniles. In a series of papers on British Columbia coho salmon, Fleming & Gross (1989, 1992, 1993, 1994) found that hatchery fish had attenuated secondary sexual characteristics, including less pronounced kypes, reduced dorsal hump height and enlarged dorsal and anal fin base sizes. Fleming &

Gross (1994) concluded that natural selection in the wild favored strong sexual dimorphism in coho salmon, with selection evidently particularly strong on body size in both sexes and on caudal peduncle depth in females and snout length in males when adjustments were made for body-size differences. These differences were smaller in hatchery fish and, as in the study by Berejikian et al. (1997), were correlated with diminished breeding success.

The morphometric differences between wild and captive adult coho salmon are more pronounced than those observed in these other studies, presumably owing to extended exposure of captive fish to a novel protective environment. Several of the morphometric characters of captive fish, e.g. reduced streamlining, increased angle of the median fins relative to the lateral line and a more forward positioning and greater separation of paired fins, may have resulted in part from elimination in captivity of the opportunity and need for sustained swimming (Fleming & Gross 1994), but possibly also to other stimuli that are absent or muted as a result of long-term confinement in circular tanks. Reduced head length, reduced snout curvature, and dorsal hump height, reveal attenuation of secondary sexual characteristics that could have resulted from a combination of environmental factors such as lack of exposure to seawater or to a migratory experience, absence of natural food, or elevated rearing densities.

We consider it likely that the distinct morphometric differences observed among these stocks are representative of those between captive and wild fish generally and in this case were largely environmentally induced. However, we cannot exclude genetic influences. An argument for environmental influences on morphometric differences between captive and wild fish is supported by three observations. First, both Stavis Creek and Big Anderson Creek captive fish, which were cultured in similar environments from parr to adult, were similar morphometrically to each other and different from Big Beef Creek fish along the primary discriminant function separating these two captive stocks from wild Big Beef Creek fish (Figure 4). Second, the two captive stocks are close geographic neighbors in the wild and, despite a lack of information on the genetic and life history characteristics of these stocks, wild fish from these stocks are likely to be similar in these respects (Berejikian et al. 1997).[5] Finally, the two wild Stavis Creek males captured in 1996 align morphometrically with wild Big Beef Creek fish based on CDA (Figure 5). Taken together, these observations imply that morphometric development in captive fish may be highly plastic and stems from differences between the captive and wild environments.

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[5] See also: Weitkamp, L.A., T.C. Wainwright, G.J. Bryant, G.B. Milner, D.J. Teel, R.G. Kope & R.S. Waples. 1995. Status review of coho salmon from Washington, Oregon, and California. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC 24. 258 pp.

Although captively reared and wild fish differed behaviorally as well as morphometrically (Berejikian et al. 1997), the consequences of morphometry for mating and spawning behavior are difficult to predict. Within groups, morphometric and behavioral traits showed poor correspondence: individual males and females exhibiting extremes of behavioral expression (Berejikian et al. 1997) were not distinctive morphometrically based on CDA. For example, correlations between partial warps and frequencies of crossovers and aggressive acts in males and spawning onset and duration of nest guarding in females (Berejikian et al. 1997) were all modest ($0.5 < r^2 < 0.7$, authors' unpublished data).

Several studies have documented a link between body size and shape and reproductive behavior of salmonids (Foote & Larkin 1988, Foote 1989, Fleming & Gross 1992, Fleming et al. 1996); our results indicate that when within-group variation is taken into account, morphometry may be only a minor factor affecting the range of reproductive behaviors in captive and wild fish. Other factors may include body coloration, social experience, and physiological state. Nevertheless, the changes in body shape and reduced sexual dimorphism associated with captive rearing (Figure 6) were correlated with limited access to females and courtship behavior in males and apparent discrimination against captive males by both wild and captive females, as well as with delayed and reduced nest construction by captive females. The wider variation in competitive ability Berejikian et al. (1997) observed between captive and wild males than between captive and wild females corresponded to a greater range of body shapes in males independent of size and may increase variation in male reproductive success (Fleming & Gross 1994, Quinn & Foote 1994).

Given the consequences of captive rearing for body shape, what are the implications for its utility as a recovery tool? Evidence is growing for salmonids that cultured fish often have lower reproductive success than wild fish in nature (Leider et al. 1990, Fleming & Gross 1992, 1993, 1994, Fleming et al. 1996, Berejikian et al. 1997, McGinnity et al. 1997), which may reduce overall productivity of naturally reproducing fish (Felsenstein 1997, Reisenbichler 1997). The morphometric changes in captive fish observed in this study appeared to result in mate selection by both captive and wild females in favor of wild males and diminished competitive ability of captive males. Although Berejikian et al. (1997) found that

both captive and wild females retained few eggs after spawning, captive rearing of females may alter maturation timing, reduce physical performance, and delay spawning. The sharp reduction in sexual dimorphism of captive fish may limit mating success of naturally spawning captive males, which in turn could reduce the effectiveness of supplementation involving captively reared fish.

In a companion study, offspring of wild and captively reared coho salmon incubated together in a hatchery exhibited similar gamete viabilities and developmental characteristics to the hatching interval (S. Schroder & C. Knudsen unpublished data). Thus, reproductive success of captive fish does not appear to be limited by postzygotic mechanisms (although the extent to which genotype X environment interaction affects gamete viability and development in a stream environment is unknown). Uncertainty about the morphometric relationship to prezygotic mechanisms suggests that the design of captive rearing environments that reduce morphometric and behavioral differentiation of captive from wild fish is an important focus for research in captive rearing technology (Maynard et al. 1995).

Acknowledgements

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