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# Morphometric variation among four distinct population segments of California steelhead trout

Farhat S. Bajjaliya*, Robert G. Titus, Joe R. Ferreira, and Ronald M. Coleman

*California Department of Fish and Wildlife, Fisheries Branch, 830 S Street, Sacramento, CA 95811, USA (FSB, JRF)*

*California Department of Fish and Wildlife, Fisheries Branch, 8175 Alpine Avenue, Suite F, Sacramento, CA 95826, USA (RGT)*

*California State University, Sacramento, Department of Biological Sciences, 6000 J Street, Sacramento, CA 95819 (RGT, RMC)*

**Correspondent: Farhat.Bajjaliya@wildlife.ca.gov*

Salmonid morphology can vary due to many factors including phenotypic expression in response to immediate environment, anthropogenic influences such as artificial propagation, and difficulty and distance of spawning migration. Because reproductive homing minimizes genetic interchange and promotes the maintenance of local adaptations, morphology of adult steelhead trout (*Oncorhynchus mykiss*) should be distinguishable between geographically isolated populations. The objective of this study was to compare adult steelhead trout morphometrics among four distinct population segments in California, including both coastal and inland populations groups. This study is the first to examine morphometric variation on a regional scale in California. We predicted that means of each morphometric response variable—body depth, fork length, and weight—would differ statistically by distinct population segment, sex, origin, and by the interactions of these factors. Adult steelhead trout were sampled at 11 locations in four distinct population segments over two sampling seasons, yielding a sample size of 4,986 steelhead trout. We found significant trends among distinct population segments, including a clear morphological distinction between coastal and inland populations where, on average, steelhead trout in coastal populations were significantly larger and morphologically more robust than those in inland populations. The Nimbus Hatchery stock within the Central Valley Distinct Population Segment was a notable exception that included, on average, the largest and most robust steelhead trout observed in this study. It is important to understand how adult steelhead trout morphology not only varies among and within geographically isolated populations, but also how morphology functions as a locally adapted life history trait, which will aid fishery managers in establishing instream flow requirements that accommodate passage of larger bodied individuals, and may also aid in the successful replacement of out-of-basin broodstocks with others exhibiting morphological traits in agreement with local environmental conditions.

Key words: California, distinct population segment, instream flow, morphometrics, Nimbus Hatchery, *Oncorhynchus mykiss*, steelhead trout

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In biology, morphology is defined as the quantitative description, analysis, and interpretation of shape and shape variation (Rohlf 1990). Morphometric methods can be utilized when it is necessary to describe and compare shapes of individual organisms within and among conspecific populations (Rohlf and Marcus 1993). Morphology of individuals can vary due to many factors, including geographic origin, phenotypic expression in response to immediate environment, sexual dimorphism, and anthropogenic influence such as artificial propagation (Beacham and Murray 1985, Fleming and Gross 1994, Hard et al. 2000).

Previous studies involving members of the family Salmonidae have shown that environmental conditions, such as difficulty and distance of spawning migration, influence the distribution of morphometrics between geographically isolated populations (Beacham and Murray 1987, Fleming and Gross 1989, Quinn et al. 2001, Kinnison et al. 2003, Quinn 2005, Doctor and Quinn 2009). The countervailing pressures associated with extensive spawning migrations lead to phenotypic selection favoring reductions of body depth, fecundity, and secondary sexual characteristics in both male and female salmonids (Fleming and Gross 1989, Taylor 1991, Kinnison et al. 2003). Because extensive migrations are often arduous, it is plausible that selection for a smaller, streamlined body may benefit locomotion and efficiency of migration over longer distances (Kinnison et al. 2003, Wilson et al. 2003).

Reproductive homing in anadromous salmonids minimizes genetic interchange among geographically isolated populations and promotes the maintenance of heritable genetic adaptations to local environments (Scheer 1939, Horrall 1981, McIsaac and Quinn 1988, Fleming and Gross 1989, Taylor 1991, Quinn et al. 2000, Doctor and Quinn 2009). Reproductively isolated populations exposed to little or no gene flow from other populations may experience phenotypic differentiation (Carvalho 1993). Consequently, locally adapted and maintained traits, such as morphology, should be distinguishable between geographically isolated populations of anadromous salmonids, including steelhead trout (*Oncorhynchus mykiss*) in California (Fleming 1986, Fleming and Gross 1989, Taylor 1991).

Within California, coastal populations of steelhead trout generally migrate shorter distances to spawn as compared to inland populations, which experience difficult migrations over great distances. Given the differences in migratory conditions, we would predict that morphological characteristics will be distinct between coastal and inland populations of California steelhead trout, where coastal steelhead trout may exhibit larger, deeper bodies, and inland steelhead may exhibit smaller, narrower bodies, based on previous observations with Coho salmon (*O. kisutch*) by Fleming and Gross (1989).

Although steelhead trout are widespread in California (Moyle 2002), most populations are in decline. In response to precipitous decline, the National Marine Fisheries

Service (NMFS) (Busby et al. 1996) delineated six genetically Distinct Population Segments (DPS) of steelhead trout in California (Figure 1), and subsequently listed five of them under the United States Endangered Species Act (ESA). The Northern California (Federal Register 2000), Central California Coast (Federal Register 1997), Central Valley (Federal Register 1998), and South-Central California Coast (Federal Register 1997) DPSs are listed as threatened, and the Southern California DPS is listed as endangered (Federal Register 1997). The Klamath Mountains Province DPS is the only steelhead trout DPS in California that is not federally-listed (Federal Register 2006). Distinct Population Segments are described as representing evolutionary significant units of the species that are substantially reproductively isolated from other conspecific population units and also represent an important component in the evolutionary legacy of the species (Federal Register 1991). Morphological variation of adult California steelhead trout among DPSs remains undocumented, and gaining a better understanding of how selective forces influence steelhead trout morphometrics may contribute to our ability to manage and recover the species.

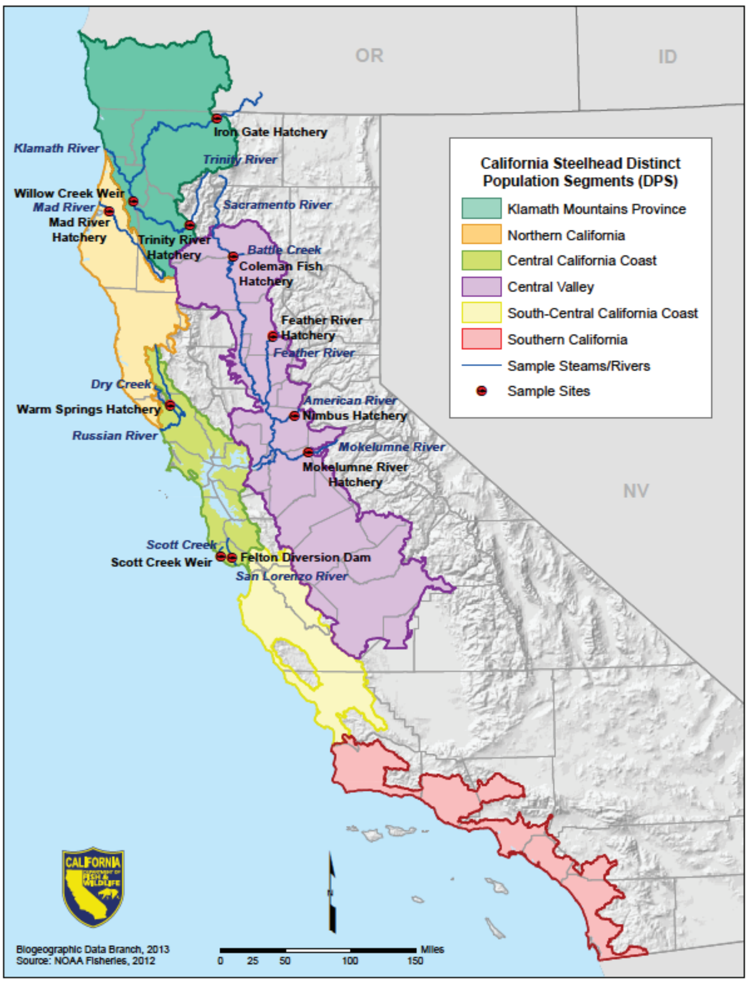


FIGURE 1.—The six steelhead trout District Population Segments and locations of study sampling sites in California.

Conservation of both coastal and inland steelhead trout populations is often associated with artificial propagation programs (Fleming and Petersson 2001, Morita et al. 2006, McClure et al. 2008, Chilcote et al. 2011). The founding broodstock used for hatchery propagation in California is usually established with individuals taken from within the same basin in which the hatchery is located. However, in some cases, hatcheries have obtained their broodstock from inter-basin transfers, which are often from a distinctly different biogeographic region than the hatchery location. Once established, the out-of-basin lineage is maintained through hatchery-produced adults returning to their hatchery of origin to be spawned (Chilcote et al. 2011).

An example in the current study is Nimbus Hatchery, located on the American River in the Central Valley DPS (Figure 1). The broodstock propagated at Nimbus Hatchery as mitigation for the Folsom Dam Project is a combination of steelhead trout native to the American River and a variety of other introduced stocks including fish from the Sacramento, Russian, and Eel rivers in California; the Washougal River in Washington; and the Siletz River in Oregon (Figure 2; McEwan and Nelson 1991, McEwan and Jackson 1996, McEwan 2001, Myrick and Cech 2005). Recent phylogeographic analysis suggests that the Nimbus Hatchery broodstock is most closely related to Eel River steelhead trout, which occurs in the Northern California DPS (Garza and Pearse 2008). What remains undocumented is to what extent the Nimbus Hatchery stock differs in morphology from the steelhead trout population that occurred in the American River prior to construction of Folsom Dam, and from other steelhead trout populations in the Central Valley DPS.


Figure 2.—Locations of the six Pacific coast rivers that provided stock used to develop steelhead trout broodstock at the Nimbus Hatchery on the American River, California.

Instream flow characteristics are another management concern related to morphometrics of steelhead trout. Like other Pacific salmonids, steelhead trout require sufficient stream discharge for maintenance of their freshwater habitat, including for migration, spawning, and juvenile rearing (Vadas 2000), and previous studies have shown that variance in stream flow between populations may play a role in local adaptation (Taylor 1991). For instance, variance in stream velocities influences prolonged swimming performance and holding ability among populations of juvenile salmonids (Riddell and Leggett 1981, Taylor and McPhail 1985b, Taylor 1991). In adult salmonids, variance in stream velocities affects morphology, where salmonids in faster flowing or headwater streams exhibit more streamlined bodies when compared to individuals in slower streams or those closer to the ocean (Riddell and Leggett 1981, Taylor and McPhail 1985a, Taylor 1991).

There is also evidence that stream discharge is associated with the abundance of returning adult salmonids, and may also affect selection for body size given that less-than-optimal flows interfere with returns of larger-bodied individuals (Mitchell and Cunjack 2007). Many steelhead trout streams in California are over-appropriated for instream water resources and, while provisions exist to protect instream flows (McEwan and Jackson 1996), the science that informs implementation of these provisions is often inadequate (Castleberry et al. 1996). Gaining a clear understanding of how adult steelhead trout morphometrics differ among DPSs will provide information for determining adequate instream flows for upstream passage of adult steelhead trout on their spawning migrations in both coastal and inland watersheds.

The objective of this study was to compare morphometrics of adult steelhead trout among four DPSs in California. Sampling locations (Figure 1) focused on hatcheries and weirs where adult steelhead trout, of both hatchery and natural origin, are intercepted annually in fishery management activities. Several factors may affect steelhead trout morphometrics, but three were chosen for analysis: geographic location, including the Klamath Mountains Province, Northern California, Central California Coast, and Central Valley DPSs; sex; and reproductive origin (natural or hatchery origin). Morphometric response variables were body depth, weight, and fork length. Fork length and weight serve as independent indices of the overall size of steelhead trout, whereas the interaction between fork length and weight, along with body depth, provide indices of body robustness (Anderson and Neumann 1996, Jones et al. 1999).

We tested the hypotheses that (1) there is a significant difference in mean body depth, fork length, and weight of adult steelhead trout among DPSs; (2) there is a significant difference in mean body depth, fork length, and weight between adult male and female steelhead trout; (3) there is a significant difference in mean body depth, fork length, and weight between adult steelhead trout of natural and hatchery origin; and (4) there are significant interactions between DPS, sex, and origin that influence the mean of each morphometric response variable: fork length, weight, and body depth.

## Materials and Methods

*Sampling locations*.—Adult steelhead trout were sampled at 11 locations in the Klamath Mountains Province, Northern California, Central California Coast, and Central Valley DPSs. Sampling in the Klamath Mountains Province DPS occurred at Iron Gate Hatchery on the Klamath River (Siskiyou County), Trinity River Hatchery (Trinity County), and Willow Creek Weir on the lower Trinity River (Humboldt County). Sampling in the

Northern California DPS occurred at Mad River Hatchery in Humboldt County. In the Central California Coast DPS, steelhead trout were sampled at Warm Springs Hatchery on the Russian River (Sonoma County), and Scott Creek Weir and Felton Dam on the San Lorenzo River (Santa Cruz County). Sampling in the Central Valley DPS occurred at Coleman National Fish Hatchery on Battle Creek (Shasta County) in the upper Sacramento River Basin, Feather River Hatchery on the Feather River (Butte County), Nimbus Hatchery on the American River (Sacramento County), and Mokelumne River Hatchery on the Mokelumne River (San Joaquin County).

Sampling occurred over two steelhead trout spawning seasons (December 2010 to March 2011 and December 2011 to March 2012) to obtain an adequate sample size for each location (Table 1). Willow Creek Weir was added during the second field season to supplement the Klamath Mountains Province DPS dataset with additional steelhead trout of natural origin. Adults encountered at Willow Creek Weir were marked with a spaghetti tag and were not resampled if encountered at the Trinity River Hatchery in the upper basin. Felton Dam and Scott Creek Weir were added as sampling locations during the second season to provide data on steelhead trout in the southernmost portion of the Central California Coast DPS.

**Table 1**.—Sample size of adult steelhead trout for each sampling location, by Distinct Population Segment.

| | | Hatchery Origin Steelhead Trout (*n*) | | Natural Origin Steelhead Trout (*n*) | | |
|---|---|---|---|---|---|---|
| Distinct Population Segment | Sampling Location | Male | Female | Male | Female | Total for Location |
| Klamath Mountains Province | Iron Gate Hatchery | 59 | 53 | 1 | 3 | 116 |
| | Trinity River Hatchery | 311 | 421 | 6 | 8 | 746 |
| | Willow Creek Weir | 1 | 1 | 55 | 41 | 98 |
| | DPS Totals | 371 | 475 | 62 | 52 | 960 |
| Northern California | Mad River Hatchery | 268 | 488 | 15 | 33 | 804 |
| | DPS Totals | 268 | 488 | 15 | 33 | 804 |
| Central Valley | Coleman National Fish Hatchery | 283 | 317 | 103 | 141 | 844 |
| | Feather River Hatchery | 247 | 251 | 46 | 12 | 556 |
| | Nimbus Hatchery | 276 | 274 | 58 | 35 | 643 |
| | Mokelumne River | 193 | 192 | 5 | 1 | 391 |
| | DPS Totals | 999 | 1034 | 212 | 189 | 2434 |
| Central California Coast | Warm Springs Hatchery | 358 | 178 | 16 | 6 | 558 |
| | Felton Diversion Dam | 43 | 44 | 34 | 55 | 176 |
| | Scott Creek Weir | 4 | 3 | 13 | 21 | 41 |
| | DPS Totals | 405 | 225 | 63 | 82 | 775 |

*Data collection*.—Adult steelhead trout were measured for body depth (mm), fork length (FL, mm), and weight (0.01 kg). Body depth was measured using a large caliper while holding the fish vertically by the tail. The measurement was made from the anterior insertion of the dorsal fin to the ventral surface of the fish, along an axis perpendicular to the lateral line.

With the exception of Warm Springs Hatchery, measurements at all locations were taken from both male and female steelhead trout in pre-spawned condition. This was not possible at Warm Springs Hatchery due to the hatchery protocol specific to this location. At Warm Springs Hatchery, measurements were taken from pre-spawned females and post-spawned males. We assumed the difference in weight and body depth between pre- and post-spawned males was negligible.

The sex (i.e., male or female) and origin (i.e., hatchery or natural) were also recorded for each steelhead trout from which morphometric data were collected. Sex was determined primarily through the expression of milt and eggs from males and females, respectively, but also by secondary sexual characteristics, such as a hooked kype in males. Origin was determined by the presence or absence of the adipose fin, given that all steelhead trout produced in hatcheries in California receive an adipose fin clip as pre-smolts prior to release.

*Sample size*.—A total of 2,182 adult steelhead trout was sampled during the 2010–2011 spawning season, and 2,804 were sampled during the 2011–2012 spawning season, yielding a total sample size of 4,986 steelhead trout (Table 1). Sampling occurred every other week at most hatcheries in both years, and on a continuous basis at Willow Creek, Felton Dam, and Scott Creek. Resampling was avoided by marking each fish with a caudal fin clip as they entered a hatchery or were trapped at a weir or dam. Iron Gate Hatchery was not sampled in 2011–2012 due to a lack of returning steelhead trout.

*Statistical analysis*.—Factorial Analysis of Variance (ANOVA) was used to analyze the various factor and morphometric response variables examined in this study. Assumptions of normality and homogeneity of variances were not always met with the data. However, Factorial ANOVA is robust and can adequately address departures from these assumptions when sample sizes are large (Table 1) because of the asymptotic properties of the central limit theorem (Zar 1999). Factorial ANOVA results were then corroborated with non-parametric resampling methods, the details of which are reported in Bajjaliya (2014, Appendix B).

We ran the Factorial ANOVAs to include both main factor effects and factor interactions. Because we found that there were significant interactions between factors (i.e., DPS, sex, and origin) for each morphometric response variable (i.e., body depth, fork length, and weight), we conducted a series of pairwise *t*-tests as post hoc analysis to determine where specific differences occurred. Pairwise *t*-tests were corrected for type I errors to preserve the overall alpha of $P \leq 0.05$. The Sidak adjustment method (Sokal and Rohlf 2012) was chosen, because only a subset of all pairwise comparisons was tested. To visually ascertain the dependency relationships between factors, two- and three-way interaction plots were generated (Figures 3–5). Interaction plots included the relationship between origin, DPS, and sex for each morphometric response variable.

We conducted a series of one-way ANOVAs to gain a better understanding of how morphometrics of Nimbus Hatchery steelhead trout compared to the morphometrics of steelhead trout in the Northern California DPS, their DPS of origin, as well as the rest of the Central Valley DPS, to which they were introduced. The ANOVAs compared the mean of each morphometric response variable (i.e., body depth, fork length, and weight) among these groups. When ANOVA results led to rejection of the null hypothesis that the means of a response variable were equal among these groups, post hoc pairwise *t*-tests using the Sidak adjustment were used to determine where the differences existed. Graphical analysis was also used to assess differences using dot plots of mean body depth, weight, and fork length with 95% *CI*s for each location.

## Results

An overview of summary statistics for body depth, weight, and fork length suggested that there were significant differences in morphometric response variables between DPSs

**Table 2**.—Summary table of statistics for each steelhead trout response variable (body depth, weight, fork length) by Distinct Population Segment (DPS).

| Response Variable | DPS | Origin | Sex | *n* | Average | *SD* | Min | Max | Skewness | *CV* |
|---|---|---|---|---|---|---|---|---|---|---|
| Body Depth (mm) | Northern California | Hatchery | Female | 488 | 134.6 | 10.5 | 98 | 180 | 0.11 | 0.08 |
| | | | Male | 268 | 141.6 | 12.7 | 104 | 184 | 0.17 | 0.09 |
| | | Natural | Female | 33 | 135.7 | 17.7 | 67 | 188 | -0.99 | 0.13 |
| | | | Male | 15 | 145.3 | 14.1 | 125 | 173 | 0.32 | 0.10 |
| | Central California Coast | Hatchery | Female | 225 | 137.6 | 13.1 | 98 | 169 | -0.53 | 0.10 |
| | | | Male | 405 | 129.9 | 20.6 | 82 | 187 | 0.03 | 0.16 |
| | | Natural | Female | 82 | 115.3 | 19.0 | 65 | 153 | -0.07 | 0.16 |
| | | | Male | 63 | 122.4 | 26.3 | 52 | 178 | -0.10 | 0.21 |
| | Klamath Mountains Province | Hatchery | Female | 474 | 112.1 | 11.6 | 83 | 153 | 0.38 | 0.10 |
| | | | Male | 370 | 121.3 | 14.1 | 84 | 161 | 0.15 | 0.12 |
| | | Natural | Female | 52 | 114.8 | 13.3 | 89 | 148 | 0.60 | 0.12 |
| | | | Male | 61 | 118.6 | 13.0 | 87 | 149 | 0.41 | 0.11 |
| | Central Valley | Hatchery | Female | 1032 | 116.1 | 18.3 | 78 | 167 | 0.39 | 0.16 |
| | | | Male | 994 | 125.0 | 19.7 | 80 | 191 | 0.58 | 0.16 |
| | | Natural | Female | 189 | 101.9 | 22.3 | 56 | 183 | 0.96 | 0.22 |
| | | | Male | 210 | 114.5 | 25.8 | 69 | 181 | 0.45 | 0.23 |
| Weight (kg) | Northern California | Hatchery | Female | 488 | 3.4 | 0.7 | 1.5 | 7.6 | 0.90 | 0.20 |
| | | | Male | 267 | 3.5 | 0.8 | 1.6 | 6.7 | 0.64 | 0.22 |
| | | Natural | Female | 33 | 3.6 | 1.0 | 0.5 | 7.3 | 0.59 | 0.28 |
| | | | Male | 15 | 3.7 | 1.0 | 2.5 | 6.1 | 0.97 | 0.27 |
| | Central California Coast | Hatchery | Female | 225 | 3.7 | 0.8 | 1.2 | 5.5 | -0.40 | 0.22 |
| | | | Male | 404 | 3.0 | 1.2 | 0.8 | 7.4 | 0.28 | 0.40 |
| | | Natural | Female | 80 | 2.4 | 1.2 | 0.7 | 7.0 | 0.99 | 0.48 |
| | | | Male | 63 | 2.5 | 1.5 | 0.3 | 6.6 | 0.53 | 0.57 |
| | Klamath Mountains Province | Hatchery | Female | 475 | 2.2 | 0.6 | 0.8 | 4.6 | 0.76 | 0.28 |
| | | | Male | 370 | 2.4 | 0.8 | 0.8 | 4.9 | 0.57 | 0.32 |
| | | Natural | Female | 52 | 2.4 | 0.8 | 1.0 | 4.2 | 0.75 | 0.31 |
| | | | Male | 62 | 2.6 | 0.8 | 1.1 | 5.8 | 1.28 | 0.32 |
| | Central Valley | Hatchery | Female | 1019 | 2.1 | 1.1 | 0.5 | 5.5 | 0.95 | 0.51 |
| | | | Male | 975 | 2.3 | 1.3 | 0.6 | 8.1 | 1.23 | 0.56 |
| | | Natural | Female | 188 | 1.5 | 1.1 | 0.1 | 6.3 | 1.98 | 0.73 |
| | | | Male | 210 | 1.8 | 1.3 | 0.5 | 6.5 | 1.44 | 0.73 |
| Fork Length (mm) | Northern California | Hatchery | Female | 488 | 668.8 | 40.7 | 512 | 890 | 0.45 | 0.06 |
| | | | Male | 267 | 692.9 | 51.0 | 523 | 898 | 0.24 | 0.07 |
| | | Natural | Female | 33 | 679.5 | 71.5 | 370 | 857 | -1.92 | 0.11 |
| | | | Male | 15 | 699.1 | 54.8 | 613 | 813 | 0.36 | 0.08 |
| | Central California Coast | Hatchery | Female | 225 | 687.1 | 51.1 | 480 | 781 | -0.98 | 0.07 |
| | | | Male | 405 | 643.7 | 89.0 | 462 | 898 | -0.10 | 0.14 |
| | | Natural | Female | 82 | 594.5 | 91.4 | 340 | 870 | -0.05 | 0.15 |
| | | | Male | 63 | 610.1 | 118.7 | 280 | 860 | -0.34 | 0.19 |
| | Klamath Mountains Province | Hatchery | Female | 474 | 596.7 | 63.3 | 398 | 764 | -0.41 | 0.11 |
| | | | Male | 368 | 617.6 | 75.7 | 395 | 805 | -0.67 | 0.12 |
| | | Natural | Female | 52 | 594.5 | 59.5 | 462 | 728 | -0.01 | 0.10 |
| | | | Male | 62 | 617.2 | 64.8 | 451 | 784 | 0.18 | 0.11 |
| | Central Valley | Hatchery | Female | 1030 | 546.7 | 94.2 | 375 | 882 | 0.79 | 0.17 |
| | | | Male | 997 | 566.6 | 106.8 | 398 | 915 | 0.89 | 0.19 |
| | | Natural | Female | 189 | 459.5 | 100.8 | 230 | 770 | 0.82 | 0.22 |
| | | | Male | 212 | 505.1 | 121.4 | 330 | 895 | 0.98 | 0.24 |

(Table 2). Significant, high-order interactions were detected between the factors in the analysis for each morphometric response variable. The three-way factor interaction for both body depth ($F_{3,4888}$=5.27) and for weight ($F_{3,4888}$=4.26) were significant (both $P$<0.001; Table 2). Several two-way interactions were significant for fork length. These included interactions between DPS and sex ($F_{3,4888}$=21.07); DPS and origin ($F_{3,4888}$=27.67); and sex and origin ($F_{1,4888}$=10.50) (all $P$<0.001; Table 3). Detection of significant factor interactions implied that response values for one factor were dependent on the values of other factors. Therefore, the factors had to be interpreted simultaneously, and not individually, during post hoc analysis.

**Table 3**.—Factorial Analysis of Variance summary table for each steelhead trout response variable (body depth, weight, fork length).

| Morphometric Response Variable | *df* | Sum Sq | Mean Sq | *F* | *P*-value |
|---|---|---|---|---|---|
| Fork Length (mm) | | | | | |
| DPS | 3 | 13807773 | 4602591 | 620.6 | < 0.001 |
| Sex | 1 | 259702 | 259702 | 35.0 | < 0.001 |
| Origin | 1 | 1572454 | 1572454 | 212.0 | < 0.001 |
| DPS:Sex | 3 | 468943 | 156314 | 21.1 | < 0.001 |
| DPS:Origin | 3 | 615810 | 205270 | 27.7 | < 0.001 |
| Sex:Origin | 1 | 77927 | 77927 | 10.5 | 0.001 |
| DPS:Sex:Origin | 3 | 43712 | 14571 | 2.0 | 0.117 |
| Residuals | 4888 | 36251052 | 7416 | | |
| Body Depth (mm) | | | | | |
| DPS | 3 | 291700 | 97233 | 318.9 | < 0.001 |
| Sex | 1 | 55944 | 55944 | 183.5 | < 0.001 |
| Origin | 1 | 48843 | 48843 | 160.2 | < 0.001 |
| DPS:Sex | 3 | 28205 | 9402 | 30.8 | < 0.001 |
| DPS:Origin | 3 | 20341 | 6780 | 22.2 | < 0.001 |
| Sex:Origin | 1 | 2261 | 2261 | 7.4 | 0.007 |
| DPS:Sex:Origin | 3 | 4824 | 1608 | 5.3 | 0.001 |
| Residuals | 4888 | 1490486 | 305 | | |
| Weight (kg) | | | | | |
| DPS | 3 | 1412.1 | 470.7 | 449.3 | < 0.001 |
| Sex | 1 | 5 | 5.0 | 4.8 | < 0.001 |
| Origin | 1 | 102.5 | 102.5 | 97.9 | < 0.001 |
| DPS:Sex | 3 | 63.2 | 21.1 | 20.1 | < 0.001 |
| DPS:Origin | 3 | 83.2 | 27.7 | 26.5 | < 0.001 |
| Sex:Origin | 1 | 10.5 | 10.5 | 10.0 | 0.001 |
| DPS:Sex:Origin | 3 | 13.4 | 4.5 | 4.5 | 0.005 |
| Residuals | 4888 | 5120.6 | 1.1 | | |

*Body depth*.—Within the Central California Coast DPS, hatchery-origin females had significantly deeper body depths than hatchery-origin males ($t$=5.7, $df$=617, $P$<0.001). In contrast, hatchery-origin males had significantly deeper body depths than hatchery-origin females in the Central Valley ($t$=-10.6, $df$=2007, $P$<0.001), Klamath Mountains Province ($t$=-10.2, $df$=712, $P$<0.001), and Northern California ($t$=-7.6, $df$=469, $P$<0.001) DPSs (Figure 3A).

Within the Central Valley DPS, natural-origin males had significantly deeper body depths than natural-origin females ($t$=-5.2, $df$=399, $P$<0.001) (Figure 3B). Hatchery-origin females had significantly deeper body depths than natural-origin females within the Central California Coast ($t$=9.8, $df$=111, $P$<0.001) and Central Valley ($t$=8.3, $df$=236, $P$<0.001) DPSs (Figure 3C). Within the Central Valley DPS, hatchery-origin males had significantly deeper body depths than natural-origin males ($t$=5.6, $df$=266, $P$<0.001) (Figure 3D). In summary, body depth varied significantly between DPSs. However, results for body depth were not consistent for the other factor variables, sex and origin.

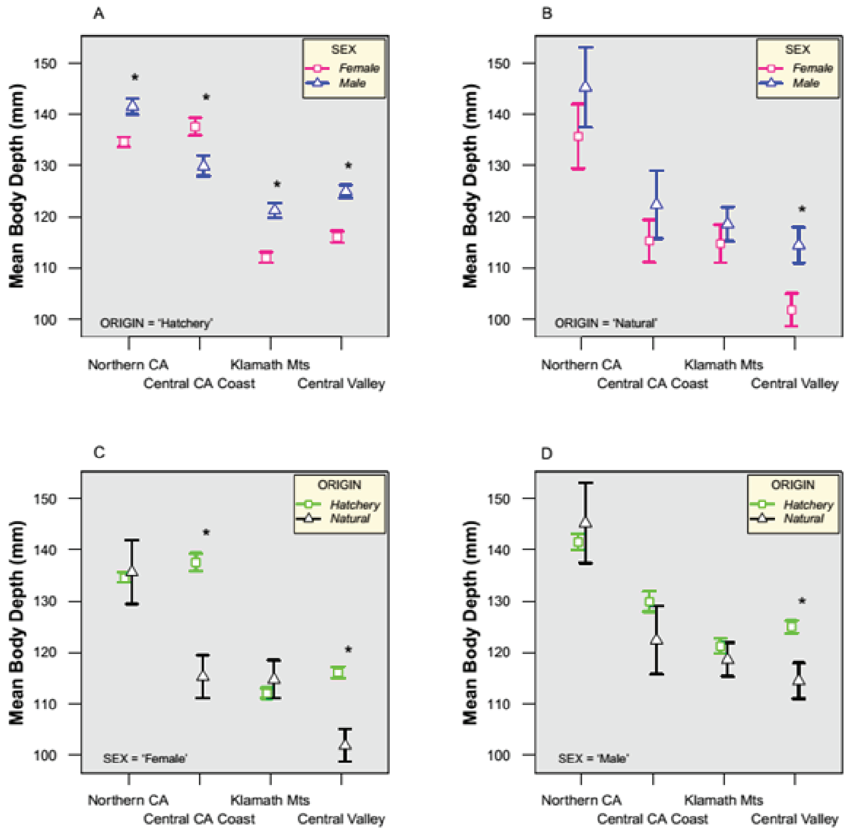


**Figure 3**.—Three-way factor interaction post-hoc results for body depth. An asterisk indicates a significant difference between the two groups at alpha=0.05. (A) Distribution of mean body depth between hatchery-origin steelhead trout females and hatchery-origin males by Distinct Population Segments (DPS). (B) Distribution of mean body depth between natural-origin females and natural-origin males by DPS. (C) Distribution of mean body depth between hatchery-origin females and natural-origin females by DPS. (D) Distribution of mean body depth between hatchery-origin males and natural-origin males by DPS.

*Weight*.—Within the Central California Coast DPS, hatchery-origin females were significantly heavier than hatchery-origin males ($t$=8.6, $df$=603, $P$<0.001). In contrast, hatchery-origin males were significantly heavier than hatchery-origin females within the Klamath Mountains Province DPS ($t$=-4.0, $df$=706, $P$<0.001) (Figure 4A). Within the Central California Coast ($t$=9.3, $df$=112, $P \leq 0.001$) and Central Valley ($t$=7.9, $df$=263, $P \leq 0.001$) DPSs, hatchery-origin females were significantly heavier than natural-origin females (Figure 4C). Within the Central Valley DPS, hatchery-origin males were significantly heavier than natural-origin males ($t$=4.6, $df$=300, $P$<0.001) (Figure 4D). In summary, as with body depth, weight varied significantly between DPSs. However, results for weight were not consistent for the other factor variables, sex and origin.

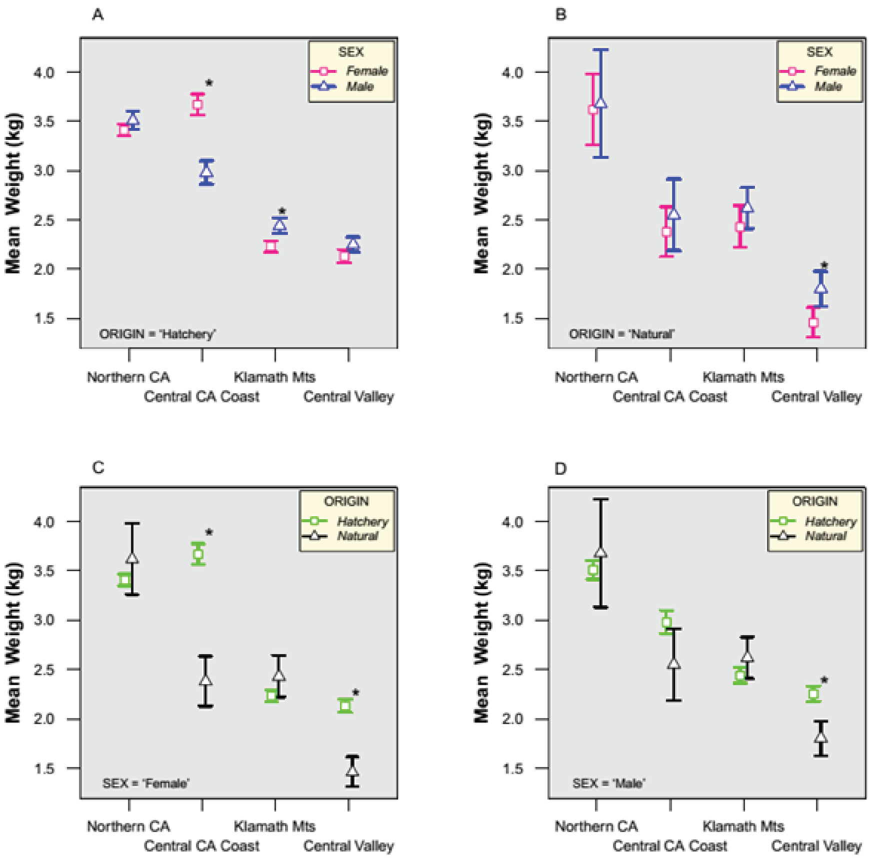


FIGURE 4.—Three-way factor interaction post-hoc results for weight. An asterisk indicates a significant difference between the two groups at alpha=0.05. (A) Distribution of mean weight between hatchery-origin steelhead trout females and hatchery-origin males by Distinct Population Segments (DPS). (B) Distribution of mean weight between natural-origin females and natural-origin males by DPS. (C) Distribution of mean weight between hatchery-origin females and natural-origin females by DPS. (D) Distribution of mean weight between hatchery-origin males and natural-origin males by DPS.

*Fork length*.—Within the Central California Coast ($t$=7.3, $df$=773, $P$<0.001) and Central Valley ($t$=15.4, $df$=2,434, $P$<0.001) DPSs, hatchery-origin steelhead had significantly greater fork lengths than natural-origin steelhead (Figure 5A). Within the Central California Coast DPS, females had significantly greater fork lengths than males ($t$=3.66, $df$=773, $P$<0.001). In contrast, males had significantly greater fork lengths than females within the Central Valley ($t$=-6.44, $df$=2,439, $P$<0.001), Klamath Mountains Province ($t$=-3.75, $df$=959, $P$<0.001), and Northern California ($t$=-3.72, $df$=802, $P$<0.001) DPSs (Figure 5B).

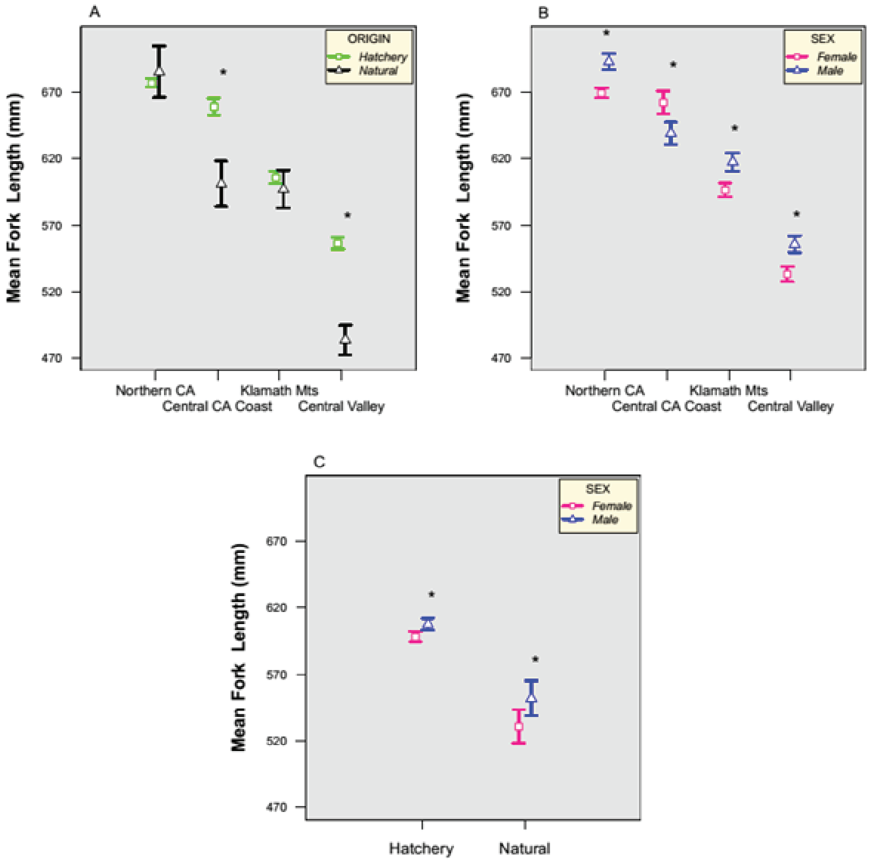


FIGURE 5.—Two-way factor interaction post-hoc results for fork length. An asterisk indicates a significant mean difference between the two groups at alpha=0.05. (A) Distribution of mean fork length between origin and Distinct Population Segment (DPS). (B) Distribution of mean fork length between sex and DPS. (C) Distribution of mean fork length between sex and origin.

Hatchery-origin males had significantly greater fork lengths than hatchery-origin females ($t$=-3.5, $df$=4,263, $P$<0.001). Natural-origin males had significantly greater fork lengths than natural-origin females ($t$=-3.3, $df$=706, $P$<0.001) (Figure 5C). In summary, as with body depth and weight, fork length varied significantly between DPSs. However, results for fork length were not consistent for the other factor variables, sex and origin.

In the comparative analysis of morphometrics that split out Nimbus Hatchery steelhead trout, there were significant differences in body depth ($F_{2,\ 3233}$=1,710), weight ($F_{2,\ 3199}$=4,051), and fork length ($F_{2,\ 3234}$=5,057) between the Nimbus Hatchery group, the Northern California DPS, and the Central Valley DPS excluding Nimbus Hatchery (all $P$<0.001). Post hoc analysis (Table 4; Figure 6) indicated that Nimbus Hatchery steelhead trout were significantly larger than steelhead trout within the Northern California DPS

Table 4.—Factorial Analysis of Variance summary table for each steelhead trout response variable (body depth, weight, fork length). Data used were from the Central Valley Distinct Population Segment excluding the Nimbus Hatchery stock, the Northern California Distinct Population Segment, and the Nimbus Hatchery stock exclusively.

| Morphometric Response Variable | Group One | Group Two | Group One ($\bar{x}$) | Group Two ($\bar{x}$) | Diff. Avg. | LCL | UCL | *t* | *DF* | *P*-value |
|---|---|---|---|---|---|---|---|---|---|---|
| Body Depth | Northern CA | Nimbus | 137.2 | 143.1 | -5.9 | -7.6 | -4.2 | -8.2 | 1243 | <0.001 |
| Body Depth | CV-No Nimbus | Nimbus | 109.6 | 143.1 | -33.4 | -35.0 | -31.8 | -49.3 | 1164 | <0.001 |
| Body Depth | CV-No Nimbus | Northern CA | 109.6 | 137.2 | -27.5 | -28.9 | -26.2 | -49.3 | 1893 | <0.001 |
| Weight | Northern CA | Nimbus | 3.5 | 3.8 | -0.3 | -0.4 | -0.2 | -7.0 | 1219 | <0.001 |
| Weight | CV-No Nimbus | Nimbus | 1.5 | 3.8 | -2.3 | -2.4 | -2.2 | -60.3 | 789 | <0.001 |
| Weight | CV-No Nimbus | Northern CA | 1.5 | 3.5 | -2.0 | -2.0 | -1.9 | -69.1 | 1160 | <0.001 |
| Fork Length | Northern CA | Nimbus | 677.8 | 695.1 | -17.3 | -24.7 | -9.9 | -5.6 | 1130 | <0.001 |
| Fork Length | CV-No Nimbus | Nimbus | 490.4 | 695.1 | -204.6 | -212.0 | -198.0 | -70.9 | 967 | <0.001 |
| Fork Length | CV-No Nimbus | Northern CA | 490.4 | 677.8 | -187.3 | -192.0 | -182.0 | -89.0 | 1738 | <0.001 |

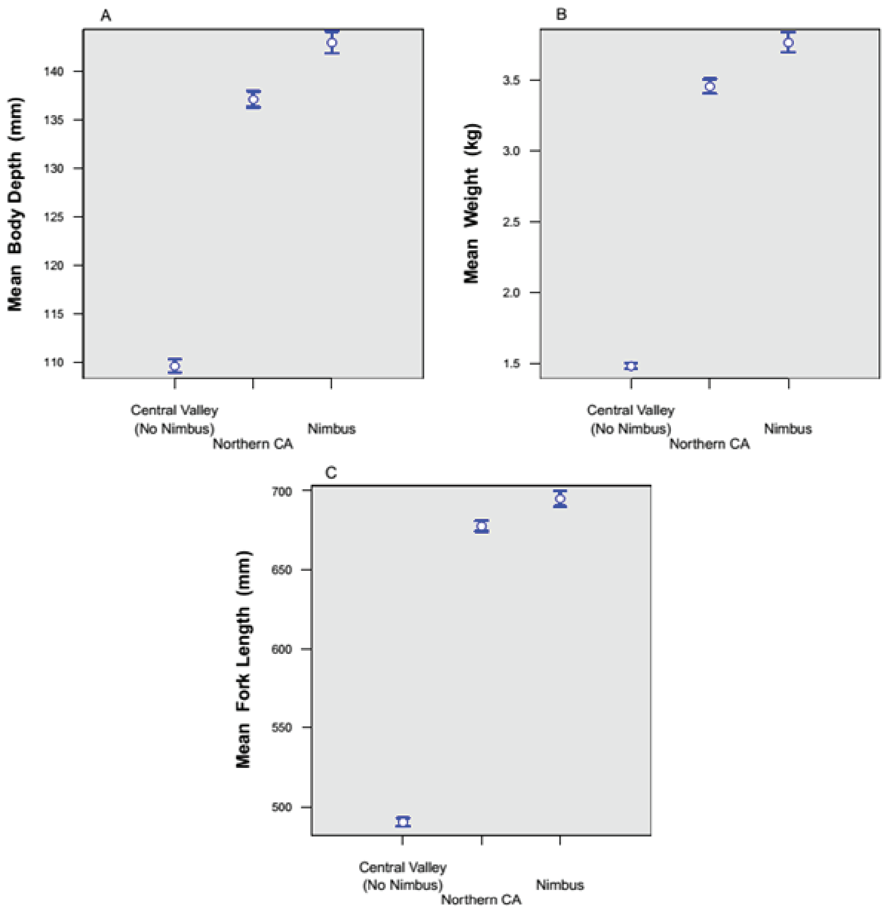


Figure 6.—Post-hoc 95% confidence intervals for the mean response by Central Valley and Nimbus Hatchery sampling locations. (A) Distribution of mean body depth. (B) Distribution of mean weight. (C) Distribution of mean fork length.

in terms of body depth ($t$=-8.2, $df$=1243, $P$<0.001), weight ($t$=-7.0, $df$=1219, $P$<0.001), and fork length ($t$=-5.6, $df$=1130, $P$<0.001). This same pattern existed between Nimbus Hatchery and Central Valley DPS steelhead trout in terms of body depth ($t$=-49.3, $df$=1164, $P$<0.001), weight ($t$=-60.3, $df$=789, $P$<0.001), and fork length ($t$=-70.9, $df$=967, $P$<0.001). Lastly, steelhead trout within the Northern California DPS were significantly larger than steelhead trout within the Central Valley DPS excluding Nimbus Hatchery, again in all three morphometric response variables: body depth ($t$=-49.3, $df$=1893, $P$<0.001), weight ($t$=-69.1, $df$=1160, $P$<0.001), and fork length ($t$=-89.0, $df$=1738, $P$<0.001).

## Discussion

While population genetic structure of steelhead trout has been assessed on a regional scale in California (e.g., Garza and Pearse 2008, Clemento et al. 2009), the current study is the first to examine morphometric variation of California steelhead trout on a similar geographic scale. We found that measurement of just a few, simple morphological features provided a basis for distinguishing among geographically isolated populations of steelhead trout.

For example, the largest adult steelhead trout, on average, occurred in the Northern California DPS, followed by those in the Central California Coast, Klamath Mountains Province, and Central Valley DPSs. We also found an overall distinction in size between hatchery and natural-origin steelhead trout, where hatchery-origin steelhead trout were longer on average than natural-origin steelhead trout (Figure 5).

Our results also provided evidence of significant trends between coastal and inland population groups. The distance migrated from the ocean to each sampling location was considered when defining the two population groups. The shortest distance migrated from the ocean was 1 km to the Scott Creek Weir and the longest was 529 km to Coleman National Fish Hatchery. Adult steelhead trout sampled at Willow Creek Weir traveled 105 km from the ocean; however, Willow Creek Weir was considered an intermediate sampling location used to sample natural-origin steelhead trout migrating to either the upper Trinity River system or to Trinity River Hatchery. There was a 10-fold difference in mean distance traveled between coastal (28 km) and inland (278 km) sampling locations.

For the purpose of this study, coastal populations were considered those in which adult steelhead trout migrated less than 160 km to where they were sampled, while inland populations were considered those in which adult steelhead trout migrated over 160 km to where they were sampled, 160 km being the approximate midpoint between the mean distances of our coastal and inland groups of sampling locations. Based on these parameters, steelhead trout sampled from the Northern California and Central California Coast DPSs were considered to be of coastal origin, while steelhead trout sampled from the Klamath Mountains Province and Central Valley DPSs were considered to be of inland origin. Our results indicated distinct morphological differences between coastal and inland adult steelhead trout where, on average, coastal populations had greater body depths, weights, and lengths than steelhead trout in inland populations (Figures 3–5, respectively).

The Central Valley DPS allowed for the opportunity to compare morphometric variation of adult steelhead trout of both inland and coastal origin within a single DPS. Nimbus Hatchery, on the lower American River, is unique in that its broodstock is an amalgamation of many intra- and inter-basin transfers made over time. However, recent phylogeographic analysis suggests that the Nimbus Hatchery broodstock is most closely related to Eel River steelhead trout, which occurs in the Northern California DPS (Garza and Pearse 2008). What remains undocumented is to what extent the Nimbus Hatchery stock differs in morphology from the steelhead trout population that occurred in the American River prior to construction of Folsom Dam, and from other steelhead trout populations in the Central Valley DPS.

In an analysis of morphometric variation between Nimbus Hatchery steelhead trout, the Northern California DPS, and the remainder of the Central Valley DPS, we found the greatest differences in all three measures of size occurred between Nimbus Hatchery, which had the largest steelhead trout, and the Central Valley DPS, which had the smallest steelhead trout (Figure 6). Morphometrics in the Northern California DPS were intermediate in size; however, these fish grouped very closely in size with those sampled at Nimbus Hatchery (Figure 6).

One possible explanation for the very robust body morphology of Nimbus Hatchery steelhead trout may be historic selection by hatchery personnel of only the largest fish for spawning, which could have imposed strong directional selection on these fish over time (Garza and Pearse 2008). There are, however, other possible explanations as to why steelhead trout propagated at Nimbus Hatchery clearly differ in morphometric traits when compared to those comprising other populations sampled within the Central Valley DPS.

Steelhead trout life history evolution is influenced by an interacting frame network of bioenergetic constraints including growth rate, asymptotic size achieved within the riverine environment, freshwater survival, and survival to adulthood (Satterthwaite et al. 2009). It is possible that the morphometrics of Nimbus Hatchery steelhead trout are influenced, in part, by a combination of phenotypic and genotypic life history responses to the highly altered environmental conditions of the lower American River, or that these fish are be pre-adapted to respond to their new environment in such a way that promotes near optimal behavior (Satterthwaite et al. 2009).

The Folsom Dam Project has blocked access to historic spawning habitat, altered historic flow regimes, and modified downstream habitat for steelhead trout in the lower American River. The alteration of historic environmental conditions has affected seasonal water temperatures and food availability, which influence growth rates of steelhead trout (Satterthwaite et al. 2009). Food availability on the lower American River is high during summer months (June-August) and results, in part, in rapid juvenile growth, early smolting, and seaward migration at age 1 (Satterthwaite et al. 2009).

Steelhead trout in the lower American River also exhibit a highly anadromous life history, which is contrary to most populations within the Central Valley DPS (Satterthwaite et al. 2009). Although few studies have been conducted, it appears that many populations of steelhead trout in the Central Valley, and elsewhere, have diverged substantially from their historic life history strategies and now include a greater proportion of fish expressing residency in response to habitat conditions that are less supportive of anadromy (Lindley et al. 2007, McClure et al. 2008, Satterthwaite et al. 2009).

It is possible that phenotypic and genotypic responses to environmental conditions in the lower American River, favoring rapid growth, early emigration, and a high degree of anadromy also influence growth potential in the marine environment and successful return of adult steelhead trout to the riverine environment to spawn. Smolt size at ocean entry influences survivability (Ward et al. 1989, Satterthwaite et al. 2009), and there is a fecundity advantage achieved by large anadromous salmonids (Scott and Crossman 1989, Beacham and Murray 1993, Wilson et al. 2003, Quinn 2005, Satterthwaite et al. 2009). Thus, the large size and robust morphology of Nimbus Hatchery steelhead trout may not only be a consequence of the genetic linkage to the Eel River stock, but also that the Eel River stock introduction was a good match for the novel anadromous environment that the lower American River represented following construction of Folsom Dam.

The Nimbus Hatchery steelhead stock is the focal point of a fishery management and conservation dilemma. This stock supports a very successful hatchery program and recreational steelhead trout fishery, the latter of which is also supported by natural reproduction in the American River. The lower American River flows through the city of Sacramento and for steelhead trout is the fifth most fished river in California (California Department of Fish and Wildlife (CDFW), Steelhead Report and Restoration Card, unpublished data), presumably due in part to extensive public access along the American River Parkway, and because of typically reliable returns of a desirable resource. The lower American River is also unique in that it provides the angler the opportunity to catch an inland stock exhibiting larger morphometrics typically found only in coastal populations. However, NMFS considers maintaining a stock of steelhead trout with known out-of-basin derived genetics for the lower American River to be in direct conflict with recovery of the Central Valley DPS (CDFG and NMFS 2001). Moreover, Garza and Pearse (2008) suggested that the Nimbus Hatchery stock may be an impediment to recovery of Central Valley DPS steelhead trout because of its potential influence on the genetic integrity of other populations in the Central Valley DPS as the result of straying.

To address this issue, fishery managers are considering supplanting the Nimbus Hatchery stock. Replacement of the Nimbus Hatchery stock could include either introduction of steelhead trout from an extant native population within the Central Valley DPS, or reintroduction of upper American River Basin *O. mykiss* that may be genetically more similar to historic lower American River steelhead trout.

Presumably, the morphometrics of steelhead trout selected as replacement stock would reflect the smaller morphometrics of steelhead trout native to the Central Valley DPS. Steelhead trout ancestors in the upper American River Basin, while potentially having a genetic fidelity with historic lower river steelhead trout, are also likely to have adapted to local, above-barrier conditions following more than 60 years of geographic and reproductive isolation from the lower river ecosystem. Environmental conditions in the upper watershed that could contribute to local adaptation include seasonal hydrologic and temperature regimes that select against anadromy (NMFS 2014), and low stream productivity, which may preclude the growth needed to achieve the dimensions of anadromous steelhead trout (Satterthwaite et al. 2009), and perform as well in the anadromous environment of the lower American River as the extant Nimbus Hatchery stock.

The importance of locally adapted traits should be considered before attempting to supplant existing populations of steelhead trout (Taylor 1991). Previous studies have demonstrated that translocations of salmonids often fail because they are ill-suited to environmental conditions in the watershed in which they are being established (Taylor 1991). Studies have also shown adaptive variation among populations can affect swimming ability (Taylor and McPhail 1985b), homing ability (Bams 1976), and disease resistance (Gjedrem and Aulstad 1974, Taylor 1991). Thus, there is a wide range of factors, in addition to morphometrics, that needs to be taken into consideration when embarking on a steelhead trout stock supplantation.

*Instream flow considerations*.—The persistence of adult steelhead trout in a given locale is critically linked to their ability to successfully make the upstream migration in their natal stream to spawn. A high frequency of lower-than-normal flow conditions in a stream can directionally select for a reduction in morphological characteristics, thereby selecting against a population inclusive of larger-bodied individuals (Beacham and Murray 1987, Quinn et al. 2001, Mitchell and Cunjak 2007). If larger bodied individuals are not able to access natal streams due to low stream discharge, they either spawn in less-than-desirable habitat, leave to spawn in other waters, or refrain from spawning altogether. Spawning area limitations due to low flows may result in decreased opportunities for segregation between natural-origin steelhead trout and strays of hatchery origin, thus enhancing the chance of genetic introgression between the two types (Jonsson et al. 1990).

Morphometrics of adult steelhead trout could be of importance when establishing instream flow requirements that accommodate upstream passage of larger bodied individuals, both in regulated and unregulated streams. Until the 1970s, minimum instream passage flows were based on professional judgment rather than on quantified relationships between stream discharge and fish passage parameters, and were often a fixed percentage of average annual stream flow (Fraser 1972, Petts 2009). Minimum stream flows could be insufficient, as they may only accommodate individuals of average size or less within the population. Thus, knowledge of the specific morphological characteristics of the target steelhead trout population should protect the broadest range of sizes in the population by providing optimum passage flows.

The California State Water Resources Control Board (SWRCB 2010) described minimum upstream passage flows for migrating adult steelhead trout as "the flow that is protective of adult fish passage in the most limiting stream sites." Sites most often limiting passage are shallow riffles or other shallow points, such as low-head weirs or dams. The ability of adult steelhead trout to navigate past these potential barriers is determined using the Thompson Method. Application of that method determines the threshold flow at which passage of anadromous salmonids will occur by providing suitable depths and velocities in at least 25% of the total width of a critically shallow passage point, 10% of which must be contiguous (Thompson 1972, Vadas 2000). A minimum depth criterion is used on a species-specific basis.

In 2010, SWRCB proposed state-wide passage criteria, which would require the provision of flows necessary to allow passage of adult steelhead trout at critically shallow points in a stream. Specifically, the criteria would provide a minimum depth of 0.21 m in at least 25% of the total-width of the stream channel, with 10% of it contiguous at such points (SWRCB 2010). Based on body depths measured in this study, the maximum of which was 0.19 m (Table 2), this depth criterion may provide minimal, suitable passage under the majority of circumstances. Our study provides evidence that body morphology of adult steelhead trout differs significantly among the DPSs sampled. The variation in body size of adult fish was most apparent between coastal and inland populations. For this reason, determining passage criteria specific to DPSs may be more appropriate than applying state-wide criteria. In some cases, passage criteria may need to be stream-specific to meet requirements of a specific population that departs morphologically from the DPS. The lower American River is an example, where steelhead trout of Nimbus Hatchery stock origin are much larger than the average for the Central Valley DPS.

Knowledge of morphological characteristics of adult steelhead trout populations throughout California could improve development of instream flow criteria for the species. Stream flow criteria for steelhead trout passage have been prescribed by SWRCB (2010), but the ability of migrating adults to pass critically low passage points per these criteria has not been substantiated in the field. Instream flow evaluations, in conjunction with morphological analysis of steelhead trout among DPSs, should be conducted to determine suitable regional, watershed, or stream-specific stream flow criteria.

*Recommendations for future work*.—This study represented a broad-brush assessment of the morphometrics of steelhead trout across northern and central California. It included steelhead trout of both hatchery and natural origin that were sampled to varying degrees at both terminal hatcheries and natural habitat areas (i.e., at weirs and dams along upstream migration routes) within each DPS. We detected general patterns in morphometrics on a geographic basis, perhaps most distinctly between what we described as coastal and inland population groups. For example, we found that, on average, steelhead trout in coastal populations (Northern California and Central California Coast DPSs) had greater body depths, weights, and lengths than steelhead trout in inland populations (Klamath Mountains Province and Central Valley DPSs).

While the data we collected infer broadscale differences in morphometrics among DPSs, we recommend that future work more thoroughly assess morphometric variation within DPSs. For example, we found that, on average, steelhead trout in the Central Valley DPS tended to be the smallest overall among steelhead trout sampled in four DPSs. However, we also found that, within the Central Valley DPS, the Nimbus Hatchery stock of steelhead trout were the largest observed in this study, even larger than those in the Northern California DPS, which were otherwise the largest observed in this study on a DPS basis. Thus, even though the coastal California origin of the Nimbus Hatchery stock may still be the primary factor behind the large size of these steelhead trout, they nonetheless represent an extreme variation on a within-DPS basis. Had sampling in the Central Valley DPS not included Nimbus Hatchery, or possibly the lower American River, this element of morphometric diversity within the DPS likely would not have been detected.

Another notable example where significant within-DPS variation should be accounted for is in the Klamath Mountains Province DPS. With the sampling sites for this DPS located well inland on the Klamath-Trinity rivers system, we classified this DPS as inland. We found that, like the Central Valley DPS, which we also classified as inland, steelhead trout in the Klamath Mountains Province DPS tended to be smaller in morphometric response variables than in the coastal Northern California and Central California Coast DPSs. Yet, the Klamath Mountains Province DPS extends all the way to the Pacific Ocean and includes coastal drainages that would be classified as "coastal," per the provisional migration distance criterion of <160 km that we used.

The Smith River (Del Norte County) is among the coastal drainages found in the Klamath Mountains Province DPS. Based on sport fishery results, this stream is widely known for its large steelhead trout, with the California state record (12.4 kg) caught in the Smith River in 1976. Although we were unable to locate morphometric data for steelhead trout on the Smith River, these fish, by all accounts, seem to be in-line with the larger coastal phenotype observed in this study, as opposed to the smaller inland type. Thus, while DPSs generally seem relevant in distinguishing different population groups based on their genetic history (e.g., Garza and Pearse 2008, Clemento et al. 2009), the coastal type-inland type model may be more applicable with respect to morphometrics. Nevertheless, we recommend that more within-DPS variation of steelhead trout morphometrics be covered in future efforts aimed at testing this model.

From a sampling design perspective, efforts should strive to include more balanced sampling between hatcheries and natural habitat areas. Doing so would alleviate concerns about potential biases that could arise from the systematic exclusion of steelhead trout—of either hatchery or natural origin—that have a behavioral aversion to ascending a fish ladder into a hatchery. Our study relied heavily upon anadromous salmonid hatcheries with successful steelhead trout propagation programs to acquire statistically robust samples, in part because of the expense and uncertainty associated with sampling adult winter steelhead trout in natural habitat areas. We did, however, take advantage of opportunities to collect data from natural-origin steelhead trout through existing monitoring programs in natural stream areas at Willow Creek Weir on the Trinity River, Scott Creek Weir, and at Felton Diversion Dam on the San Lorenzo River.

We also recommend that future work on morphometric variation in California steelhead trout include the South-Central California Coast and Southern California DPSs. Nominally, these population groups of steelhead trout would be coastal type. However, the historic population structure in these southerly DPSs may have included complements of both the large, coastal type such as those still observed in the Carmel and Big Sur rivers in Monterey County (R. Titus, CDFW, unpublished age-and-growth data), as well as smaller, inland-type steelhead trout that may have prevailed in interior drainages, and that have been especially impacted by water diversions and other habitat limitations (Busby et al. 1996). Adult steelhead trout would have made relatively extensive migrations to reach reproduction areas in many of these interior drainages, per our provisional definition of inland-type steelhead trout. Such drainages include the Salinas River (San Luis Obispo and Monterey counties), Santa Maria and Santa Ynez rivers (Santa Barbara County), and the Santa Clara River (Ventura and Los Angeles counties), and other drainages through the southernmost distribution of steelhead trout in the eastern Pacific.

Our final recommendation for future work is to further refine the terms that we used in this study to define coastal and inland type steelhead trout. The mean migration distance inland to our sampling locations differed by an order of magnitude, averaging 28 km at coastal DPS sampling locations, and 278 km at inland DPS sampling locations. We selected 160 km as the general benchmark distance for distinguishing between coastal and inland migrations, given that it is the approximate midpoint between the mean distances of our coastal and inland groups of sampling locations. While provisional, future work should be based on an appropriate sampling design to determine distributions of migration distances to putative coastal and inland steelhead trout reproduction areas in all six California DPSs. Other environmental factors that may influence the selection of morphometrics in various population groups of steelhead trout could also be included, to develop a more comprehensive assessment of possible determinants of evolved patterns in steelhead trout morphology. Such factors may include elevation gain, hydrology, and water temperature, some or all of which could influence the selection of both physical and physiological traits of steelhead trout relative to the requirements for reproductive migration.

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