DEVELOPMENT OF A STANDARD WEIGHT EQUATION FOR JUVENILE STEELHEAD TROUT AND EFFECTS OF TEMPERATURE, TURBIDITY, AND STEELHEAD TROUT BIOMASS ON RELATIVE WEIGHT

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ABSTRACT

Development of a Standard Weight Equation for Juvenile Steelhead Trout and Effects of Temperature, Turbidity, and Steelhead Trout Biomass on Relative Weight

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Standard weight equations were developed for juvenile steelhead using the regression line percentile and empirical methods. The equation developed using the empirical method better represented juvenile steelhead lengths and weights and was free of length bias. Standard weight was used to estimate average relative weights for juvenile steelhead trout populations in northern California streams. Population averages of relative weight, estimated by the empirical equation, were then modeled against turbidity, temperature, and juvenile steelhead trout density to determine if these variables had meaningful relationships with condition.

Average relative weight measured in the fall was positively related to degree day accumulation during late winter and early spring. Turbidity and biomass metrics were not found to be significantly related to juvenile steelhead trout condition. Further research is needed to determine if relative weight accurately represents the effects of physiological, population and environmental variables on juvenile steelhead trout condition.

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INTRODUCTION

Increased size and weight in juvenile salmonids have repeatedly been linked to increased overwinter survival (Holtby 1988, Quinn and Peterson 1996) and higher survival and return rates for smolts (Ward and Slaney 1988, Ward et al. 1989, Tipping 1997). Conversely, small fish with lower lipid levels have been shown to have higher mortality rates than larger fish with higher lipid content (Biro et al. 2004).

Condition is a measure of fish size that may be useful in determining the success of a salmonid. It is thought that condition represents the physiological (Murphy et al. 1990) or nutritional (Busacker et al. 1990) state of a fish. Condition, as a measure of the plumpness of a fish, may indicate the quality of environmental conditions including habitat and prey availability (Blackwell et al. 2000). Condition indices have the potential to monitor fish health for large numbers of fish since they are non-lethal and inexpensive metrics based on length and weight (Fechhelm et al. 1995).

If the assumptions of these indices are not met, the resulting estimated condition will be erroneous. For example, one assumption of the relative condition factor is that length-weight relationships among populations being compared will have equal slopes. If this assumption is not met, the estimated condition will be a factor of length rather than the nutritional state of the fish (Bolger and Connolly 1989, Cone 1989). Despite this potential for misuse, condition indices continue to be used in management and are prevalent in the literature. Condition has been used to describe patterns in fish health, body composition, growth, prey availability, community indices (including density), and for evaluating management decisions (Blackwell et al. 2000).

Blackwell et al. (2000) and Froese (2006) reviewed a number of available condition indices and determined that not all condition factors are equally useful in monitoring (Table 1). Fulton's condition factor (K) assumes isometric growth, which is rarely true (Froese 2006). Use of relative condition factor (Kn) requires different equations for different regions, making comparisons among populations difficult (Carlander 1969). Relative condition factors may only be compared among populations with similar slopes in length-weight relationships (Bolger and Connolly 1989, Cone 1989).

The relative weight (W_r) index was developed in an attempt to address these limitations. Relative weight has been used to compare condition among fish that are different sizes or species (Ney, 1993). Increases in relative weight could imply improved environmental conditions (Murphy et al. 1990, Hubert et al. 1994) or food supply (Flickinger and Bulow 1993, Liao et al. 1995), an increase in growth (Willis 1989, Gabelhouse 1991, Guy and Willis 1995) or overwinter survival (Brown and Murphy 1991). Increased relative weight has also been linked to a decrease in fish density (Johnson et al. 1992). It can be used to estimate seasonal changes in condition related to feeding (Fechhelm 1995) or spawning season (Neumann and Murphy 1992). The relationship between relative weight and length increment has been shown to change seasonally and relative weight may better represent growth at certain times of year (Gabelhouse 1991).

Given relative weight's potential relationships with environmental variables, it could be useful in determining which parameters impact salmonid condition during their

Table 1. Comparison of condition indices. W stands for weight and L represents length for the fish in question.

Condition Index	Formula	Properties	Weaknesses
Fulton's condition factor (K)	$K = 100\frac{W}{L^3}$	• Assumes isometric growth • Varies with sex, season and degree of gonad development • Used to compare the weight of an individual to that of an ideal specimen	• Isometric growth rarely true (Froese 2006)
Relative condition factor (Kn)	$Kn = \frac{W}{aL^b}$ a = intercept, b = slope	• Compensates for changes in form with changes in length • Compares weight of the fish in question to an average weight for that length (allows for comparison of fish that are different lengths)	• Assumes the length-weight relationship remains constant over the period of study • Cannot be used to compare different populations (Carlander 1969)
Relative weight (W_r)	$W_r = 100 * \frac{W}{W_S}$, W_s is a standard weight representing the 75th percentile of weight for the length in question	• Allows for comparison of condition across fish lengths, populations and species • Compares weight of the fish in question to a standard weight for that length (allows for comparison of fish that are different lengths)	• Choice of 75th percentile as the standard for weight was arbitrary (Froese 2006) • Regression line percentile method involves extrapolating beyond measured lengths for population regressions (Murphy et al. 1990)

freshwater life history stage. This could potentially show which physical characteristics in freshwater have the greatest effect on salmonid overwinter, smolting, and survival success given the link between these factors and size. Using relative weight, populations are compared to a benchmark, the standard weight. By using the same standard for an entire species, habitat quality impacts can be estimated and compared throughout the species' range.

The life history and distribution of steelhead trout make them an appropriate species for use in determining the relationship between salmonid condition and habitat quality of coastal streams. Steelhead trout are an ideal candidate for this project because they spend from 1 to 3 years in freshwater (Moyle, 2002), so the condition of juveniles would likely reflect productivity and habitat quality of the freshwater habitat (Duffy et al. 2003).

There has been a call for further research on impacts of habitat restoration, including road removal (Switalski et al. 2004), on stream-dwelling salmonids. Road removal can influence turbidity levels in aquatic ecosystems. Increased road density and the number of road crossings in a watershed have also been shown to be linked to an increase in water temperature (expressed as maximum weekly average temperature, Nelitz et al. 2007), making temperature another variable that could be affected by habitat restorations. Turbidity and temperature are therefore two physical variables that vary throughout stream systems and should be studied further to determine their impact on condition of salmonids.

Turbidity, which is caused when suspended or dissolved material causes light to scatter or be absorbed (American Public Health Association et al. 1992), has been shown to have an effect on fish growth and size. Numerous studies have reported a decrease in growth of fish at higher turbidities or sediment concentrations (Herbert and Richards 1963, Sykora et al. 1972, Craig and Babaluk 1989, Sweka and Hartman 2001a). Increasing turbidity has also been reported to result in a decrease in feeding efficiency (Sigler et al. 1984) or to decrease reactive distance in fish (Berg and Northcote 1985, Barrett et al. 1992, Sweka and Hartman 2001b). In addition, turbidity has been shown to decrease primary and secondary production (Lloyd et al. 1987). Both the concentration of suspended sediment and duration of exposure have been found to influence the magnitude of effect on aquatic organisms. The severity of ill effects of sediment on aquatic organisms increases with increasing duration of exposure (Newcombe and MacDonald 1991, Newcombe and Jensen 1996). In one study, rainbow trout growth decreased with increasing duration of a constant concentration of sediment exposure (Shaw and Richardson 2001).

Water temperature has also been documented to affect growth and size of steelhead trout and other salmonids through effects on metabolism, behavior and mortality (Bjornn and Reiser 1991). In a multiyear observational study of salmon and trout, researchers detected an increase in fish size with an increase of water temperature expressed as degree days (up to 2390 degree days for a period of December to September) in a Scottish stream (Egglishaw and Shackley 1977). Age-0 steelhead trout fed to satiation exhibited increased growth rates at increased temperatures (up to 19º C) in a laboratory setting (Myrick and Cech 2005). Increased fall-spring temperatures (maximum temperature was approximately 11º C) were also shown to result in increased simulated growth in rainbow trout (Railsback and Rose 1999). However at extreme upper temperatures, growth may be reduced (Bjornn and Reiser 1991). Neiltz et al. (2007) estimated that juvenile rainbow trout growth would increase with increasing maximum weekly average temperature until 17º C, after which growth rates declined.

Density of fish within a stream is a population parameter that has been linked to fish size or weight. Steelhead trout and other salmonids have had lower weights and sizes (Egglishaw and Shackley 1977, Wentworth and LaBar 1984, Hume and Parkinson 1987, Keeley 2003) or decreased growth (Keeley 2001, Harvey et al. 2005) with higher fish densities. However, condition of fish does not appear to vary consistently with fish density. Condition has been reported to increase with decreased density and less competition for food (Baccante and Reid 1988). Similarly, a decrease in condition was observed with an increase in biomass due to limited prey resources (Verdiell-Cubedo et al. 2006). However, in the laboratory Winfree et al. (1998) found the lowest steelhead trout condition coinciding with low fish densities. In a review of numerous larval and juvenile studies, Cowan et al. (2000) concluded that the density-dependent regulation of growth and biomass most likely occurs in the late-larval or juvenile stage of fish, making this an appropriate life stage to study when looking at density dependent effects.

Given the documented benefits of increased size and the effects of turbidity, temperature, and density on fish size and growth, this study investigated the effects of these variables on the condition of juvenile steelhead trout (*Oncorhynchus mykiss*).

There are currently two methods to estimate relative weight: regression line percentile (Murphy et al. 1990) and empirical (Gerow et al. 2005). Both procedures use lengths and weights throughout the range of a species to derive a standard weight equation. Relative weight is derived from standard weight using the formula in Table 1.

In both the regression line percentile and empirical methods for relative weight, the standard weight is a representation of the 75th percentile of weight from populations in the developmental dataset. In their earlier relative weight methodology, Wege and Anderson (1978) used 75th percentile weights to calculate the standard weight because this value resulted in relative weights approaching 100 for “suitable values” of weight. Murphy et al. (1990) continued the use of 75th percentile weights in their development of the regression line percentile method in order to compare their results to those of Wege and Anderson and also to set a management goal of producing populations with “better-than-average” condition. However Murphy et al. (1990) warned that the standard is merely a benchmark and should not represent a universal management target.

The difference between the regression line percentile and empirical methods are in the statistical populations modeled to estimate the standard weight equation. In the regression line percentile method, $\log_{10}$ transformed weight is regressed on $\log_{10}$ transformed length for each population in the developmental dataset. The parameters of these regressions are then used to generate modeled weights which are used to develop the standard weight equation (Murphy et al. 1990). In the empirical method, the measured lengths and weights from the developmental dataset are used to generate the standard weight equation (Gerow et al. 2005). Both methods were used in this study to develop standard weight equations and the estimated equations were compared to determine which was free from length bias and whether there were differences in the relative weights estimated by the two methods.

One limitation of the standard weight method comes from extrapolating beyond the measured lengths used in the creation of the standard weight equation (Blackwell et al. 2000). In addition, the relationship between length and weight often changes as individuals undergo developmental changes (Tesch 1968). The equation developed in my study can be used for juvenile fish but would not be applicable to steelhead trout undergoing smoltification since anadromous species undergo a morphological change during smolting (Hoar 1976).

I used juvenile steelhead trout biomass as an estimate of density. Steelhead trout biomass as opposed to salmonid biomass was the chosen metric because steelhead trout have been shown to outcompete (Moyle 2002) or occupy different microhabitats than other salmonid species (Bisson et al. 1988).

The objectives of my study were to develop a standard weight equation for juvenile steelhead trout using the regression line percentile and empirical techniques, compare the equations to determine if there were differences in relative weights estimated, and to estimate the effects of turbidity, temperature and density of fish on relative weight. I estimated average relative weights for populations of juvenile steelhead trout from streams in northern California. Relative weights were modeled against turbidity, temperature, and steelhead trout density to determine if condition of steelhead trout in freshwater systems is related to these physical and population variables.

METHODS

Development of the Standard Weight Equations

To derive the standard weight equations, a dataset of juvenile steelhead trout fork length and weight data was compiled. Although differences in condition may occur throughout the geographic range of steelhead trout, it was necessary for a species-wide equation to be made to allow for comparisons between populations (Murphy et al. 1990). In North America, steelhead trout inhabit coastal streams extending from Alaska to San Mateo Creek, in San Diego County, California (Moyle, 2002). The datasets compiled represented samples of steelhead trout populations from Juneau, Alaska to San Luis Obispo, California. Length-weight datasets were gathered from a variety of sources, including federal, state, and municipal agencies, timber companies, and universities (Appendix A).

Agencies sharing data were asked to confirm that lengths and weights were obtained from wild, juvenile (pre-smolt) steelhead trout. Data from hatcheries, and marked hatchery fish (e.g. with fin clips), were not included in the developmental dataset because their condition may represent hatchery feeding schedules rather than environmental variation. Lengths and weights from fish known to be smolts were excluded because smolts undergo morphological changes before outmigration and their body shape form differs from pre-smolts (Hoar 1976). While it is possible that length weight data from some hatchery fish or smolts were included in the developmental dataset, efforts were taken to exclude data known to be from these groups.

Populations considered for the developmental dataset were assessed to ensure more than one year of data from a site, outlier length-weight pairs and populations, small datasets, and populations in which length was poorly correlated with weight were excluded (Table 2). One hundred populations were included in the developmental dataset.

The upper and lower lengths used in the standard weight equation were determined by plotting the variance of weights against fish length (Flammang et al. 1999). If there was a sudden increase in variance of weight when plotted against length in 5-mm intervals, that interval was designated to be outside the length range to which the standard weight equation can be applied.

Biological factors also need to be considered in determining the length range for a juvenile steelhead trout standard weight equation. The lower cutoff needs to consider that the geographic range for juvenile steelhead trout overlaps with that of cutthroat trout. At lengths less than 70 mm, it is difficult to distinguish between the two species. Additionally, large fish may represent resident rainbow trout rather than anadromous steelhead trout. These biological factors were considered in conjunction with Flammang's technique to determine the length range for the standard weight equations.

Standard weight equations were developed using the regression line percentile (Murphy et al. 1990) and empirical (Gerow et al. 2005) techniques. Both the regression line percentile and empirical equations were developed using the same developmental datasets over the same length range.

The regression line percentile technique treats the $\log_{10}$ transformed weight-length regressions for each population as the statistical population to be modeled. These

Table 2. Steps for selecting length-weight data from juvenile steelhead trout populations for inclusion in the developmental dataset for standard weight equations.

Step	Description
Check species and units of measure.	Remove length-weight information on non-steelhead trout species and known smolts or hatchery-raised fish. Check that fork lengths and weight were recorded in metric units.
Separate data by stream and year	Sort into populations representing one year of sampling data for each stream. For streams with multiple years of data, the year with the most length-weight pairs was the population used in the developmental dataset (Pope et al. 1995).
Delete length-weight pair outliers	Examine populations for outliers in the length-weight data points, which may have resulted from measuring or transcription error. Errors were identified by plotting $\log_{10}$ weight against $\log_{10}$ length and deleting obvious outliers (Bister et al. 2000).
Determine length range for the equation	Plot the variance of weights against fish length (Flammang et al. 1999). If there is a sudden increase in variance of weight when plotted against length in 5-mm intervals, that interval was designated outside the length range. Length-weight pairs outside of the upper and lower limits for the equation's length range were eliminated from the developmental dataset.
Delete populations with sample size < 30	Delete populations with small numbers of length-weight pairs from the developmental dataset. The literature recommends that populations in the developmental dataset have at least 10 length-weight pairs (Murphy et al. 1990, Pope et al. 1995), due to the large number and sizes of datasets available for juvenile steelhead trout, a minimum of 30 fish was used in my study.
Delete populations with weight-length correlation < 0.90[a]	Screen populations to ensure length is correlated with weight (Brown and Murphy 1996, Bister et al. 2000). The literature recommends a cutoff of 0.80 for the coefficient of determination, R^2 (Pope et al. 1995, Flammang et al. 1999). However I deleted populations from the developmental dataset if their R^2 was less than 0.90. My developmental dataset was large enough to accommodate a higher minimum correlation coefficient.
Delete populations that are outliers [b]	Plot the y-intercept as a function of slope for $\log_{10}$ transformed weight-length regressions for each population (Pope et al. 1995) and visually inspect for outliers. A box plot analysis was also conducted to determine which slopes and intercepts were outliers (Mendenhall et al. 2005). Any populations with parameters that were outliers from the rest of the developmental dataset were further examined (Pope 2006, personal communication, Willis 2006, personal communication).

[a] No populations were deleted from my developmental dataset because of low weight-length correlation.
[b] No obvious errors were detected (e.g., transcription errors) in outlier populations in my developmental dataset. In populations that had slopes or intercepts that were outliers, these values were assumed to be outliers because of variation from natural differences in condition among the populations. The populations with slopes or intercepts that were outliers were therefore not excluded from the developmental dataset.

regressions were used to predict $\log_{10}$ weights for the mid-point of each length class. Five mm length classes were used since the range of lengths in an equation for juveniles is smaller than ranges used for adult fish (Flammang et al. 1999). The modeled $\log_{10}$ weights for all regressions in the statistical population were back-transformed to weight to determine the 75th percentile of weights for the midpoint of each length class. Log_{10} transformed 75th percentile weights were regressed against $\log_{10}$ lengths to determine the parameters of the standard weight equation (Murphy et al. 1990).

The empirical method uses empirical data, rather than modeled weights, in determining the 75th percentile of weights (Gerow et al. 2005). Within each population, weights were averaged for each length class and the Blom estimator (Gerow 2009) of the third quartile of average weights was used to calculate the 75th percentile of the weights. The Blom estimator is a rank estimator used to reduce positive bias, especially for small sample sizes (Gerow et al. 2005). The Blom estimator of the third quartile was then $\log_{10}$ transformed and plotted against $\log_{10}$ transformed midpoints of the 5-mm length classes. The parameters of this regression encompass the EmP standard weight equation. Gerow et al. (2005) suggested that a better fit of the data is often attainable using a quadratic regression, so this was also developed.

After developing the regression line percentile equation, it was tested for length bias. Length bias is a systematic tendency for a standard weight equation to over- or underestimate weight with an increase in length (Gerow et al. 2004). If an equation exhibits length bias, it does not accurately represent the growth of the species.

Gerow et al. (2004) proposed the empirical quartiles method for determining length bias. In the proposed method, third quartiles of mean weights at length are estimated for each population, and standardized by the standard weight for that length. A weighted regression of the standardized third quartile weights against length is calculated. The regression is weighted by the number of populations that have data within each length class. As with the empirical standard weight equation, a quadratic regression often provides a better fit for the data. If the weighted regression results in a statistically significant relationship determined by a p-value less than 0.05, and a high coefficient of determination (R^2), the equation is determined to exhibit length bias (Gerow et al. 2004). However, Gerow et al. (2004) caution that the p-values should not be taken as the only measure of whether the standard weight equation exhibits length bias. The slope of the length bias regression should also be taken into consideration as it will indicate the degree to which the standard weight equation over- or underestimates standard weight values across length.

To determine length bias in equations developed using the empirical method, which was developed in an attempt to address such issues (Gerow et al. 2005), I plotted standardized residuals of third quartile weights for the empirical data against length. If there were no trends in increases or decreases across the length range, the equation was determined to be free of length bias. Standardized residuals were also plotted for the regression line percentile equation to compare residuals for equations derived using both methodologies.

Relative weight derived from the regression line percentile and empirical equations were estimated and plotted against length (Gerow et al. 2005). The standard of comparison used was relative weights of 100 as calculated using the empirical-derived standard weight equation. As explained by Gerow et al. (2005), deviations in relative weight values for the two equations imply that the regression line percentile equation is not accurate, either due to curvature in the data which is not captured in the linear regressions of the regression line percentile technique or length bias.

After a standard weight equation has been developed and determined to be free from length bias, it can be used to estimate relative weights of fish. Murphy et al. (1990) did not advise estimating a mean relative weight for an entire population, but rather for length classes within a population. They argued that a mean relative weight for an entire population might mask trends in relative weights across length intervals. However, for my study, the length interval over which the standard weight equation may be applied was small, representing only juvenile steelhead trout. Therefore, I included all lengths for which the equation was valid in the estimation of mean relative weights.

Modeled Data

I sampled fifteen sites to include in the analysis of relative weight, turbidity, temperature, and biomass. Two streams (Cañon Creek and Maple Creek, both sampled in 2005) had two reaches each where turbidity and temperature were recorded and fish sampling occurred. Study reaches on Cañon Creek were separated by 142 m. On Maple Creek, study reaches were 127 m apart (DeYoung 2007). Turbidity and temperature data were available for both reaches. In between the reaches were sources of turbidity input that resulted in different turbidity readings for both sites. On both Maple and Cañon Creeks, the two reaches were treated as independent data points in my analysis. Additionally, two of the streams (Bull Creek and Elder Creek) were sampled in both 2005 and 2006 and treated as independent data points in my analysis. All of the study sites were selected because of the presence of continuous in-stream turbidity gauges. All sites are located in the North Coast region of California (Table 3).

Several sites originally chosen were not used in the analysis after sampling revealed a paucity of steelhead trout ($\leq$ 7 steelhead trout in 100+ meter sections). The low numbers of steelhead trout present would not have allowed for a useful estimate of relative weight. These included Godwood Creek, Little Lost Man Creek, North Fork of Lost Man, and the Upper Prairie Creek and Prairie Creek above Boyes sites. Two additional sites were dropped because temperature data were not available (Canoe Creek and Pudding Creek).

All sites were in northern California and experience high proportions of their annual precipitation during winter, which is also when periods of higher flows and turbidity occur. Most sites exhibit mild summer and winter temperatures with average annual precipitation ranging from 102 – 178 cm. Average annual maximum air temperature is approximately 15.5º C. The one exception was Carneros Creek in Napa County, the southernmost site. Summers in the vicinity of Carneros Creek tend to be hot and dry (average annual maximum air temperature 20.5º C) and average annual precipitation is lower than the other sites (48 cm; Western Regional Climate Center

Table 3. Description of study sites.

Stream Name	Latitude of Mouth (Decimal degrees)	Longitude of Mouth (Decimal degrees)	Elevation (ft)	Upland vegetation	Basin drainage area (km^2)	Land Use
Bull Creek	40.3490	-124.0012	272	Redwood[a]	108.0	State Park
Cañon Creek	40.8349	-123.9392	200	Redwood, Douglas-fir[b, c]	42.3	Timber[d]
Carneros Creek	38.2213	-122.3119	3	Bay laurel[e]	23.0	Vineyard, grazing
Cuneo Creek	40.3338	-124.0256	381	Douglas-fir	10.8	State park
Elder Creek	39.7296	-123.6484	1342	Redwood, Douglas fir[f]	16.8	Public Reserve
Jacoby Creek	40.8435	-124.0837	3	Redwood, Douglas-fir	43.9	Residential and timber
Lost Man Creek	41.3315	-124.0317	62	Redwood	32.6	National park
Maple Creek	40.7643	-123.8884	331	Redwood, Douglas fir[c]	40.4	Timber
North Fk, Caspar Creek	39.3623	-123.7341	85	Redwood, Douglas fir	4.7	State demonstration forest
Prairie Creek	41.2998	-124.0506	39	Redwood	10.0	National park
South Fk, Caspar Creek	39.3404	-123.7517	46	Redwood, Douglas fir	4.2	State demonstration forest

[a] *Sequoia sempervirens*
[b] *Pseudotsuga menziesii*
[c] Riparian dominated by red alder (*Alnus rubra*)
[d] Timber refers to areas of commercial timber production.
[e] *Laurus nobilis*
[f] with mixed conifer and deciduous trees.

2009). Sites also represented a mix of land use history and vegetation and varied catchment area (Table 3).

To ensure that steelhead trout sampled were representative of turbidity values for each site, study reaches encompassed areas above and below turbidity gauges, with fish being sampled from reaches that were approximately 200 m. Where possible, the reach extended approximately 100 meters upstream and 100 meters downstream of the turbidity gauge. One exception was North Fork Caspar Creek which flowed into an impoundment a few meters downstream of the turbidity gauge. The impoundment was not appropriate for sampling juvenile steelhead trout, nor was it representative of the turbidity readings from the gauge. For this site, the study reach began at the gauge and extended upstream for 200 meters.

A habitat survey was conducted at each site to designate units as riffles, runs, pools, deep pools (≥ 1.1 m deep), or complex, based on modified descriptions provided by McCain et al. (1990). Deep pools were not sampled due to limitations of the backpack electrofishers used in the study. A habitat unit was termed complex if there was an abundance of woody debris or some other feature which made fish collection overly difficult or unsafe for the sampling crew. Complex habitat units were subsampled from a portion of sites.

A habitat unit was recognized if it was at least as long as the channel width (McCain et al. 1990). Habitat measurements included unit length and width. Width was determined from an average of 3-5 measurements (McCain et al. 1990). These measurements were used when calculating habitat area for use in estimating juvenile steelhead trout biomass.

Electrofishing was conducted to sample the fish populations. Vertebrate sampling procedures were approved by Humboldt State University (IACUC permit # 05/06 F.32-A). Sampling took place from late summer to early fall of 2005 (n = 10) and fall of 2006 (n = 5). Sampling at the same time of year for all sites controlled for seasonal variation in relative weight (Gabelhouse 1991, Neumann and Murphy 1992, Fechhelm et al. 1995).

Sampling was multiple pass (depletion) electrofishing, to estimate steelhead trout density. I timed sampling in late summer and early fall to increase the accuracy of density estimates, since there were fewer small, hard to catch fry and flows were lower. At least two passes were conducted on all non-complex sample habitat units. If the number of steelhead trout caught during the second pass was greater than 25% of the number of fish caught in the first pass, a third pass was also made.

Complex units were subsampled so that the relative weight value for a system was representative of steelhead trout in these units as well. For the most part, depletions were not conducted in complex units because sampling in these units was very time consuming compared to the other habitat units and also because they sometimes presented safety issues for the sampling crew (e.g. underwater obstructions).

Upper and lower portions of habitat units were blocked off with 6-mm mesh nets to ensure fish in a given habitat unit did not escape during sampling. Habitat units were chosen as the level of sampling for fish populations because of the ease of setting nets at habitat breaks. Fork length (±1.0 mm) was measured and wet weight (±0.01 g) was recorded using an electric balance. Fish species other than steelhead trout were identified and counted. Fish were put in a bucket until all had been recorded, after which they were released into the habitat unit from which they had been removed.

I attempted to capture a minimum of 100 steelhead trout from each site to estimate an average relative weight. In work with four different salmonid species, Hyatt and Hubert (2001) determined that a sample of 100 fish yielded an estimate of mean relative weight that had a confidence interval width less than 4 relative weight units. To obtain this number of fish, habitat units were subsampled, starting with the first unit of each habitat type. Every third pool, run and riffle were sampled. If fish numbers were sufficiently low in the first habitat units to suggest that 100 steelhead trout would not be caught using subsampling, all units were sampled. If all habitat units were sampled in both 100-meter reaches and 100 fish still had not been captured, additional habitat units were sampled until 100 steelhead trout were caught, unless this would have resulted in too great an effort given constraints of the sampling schedule.

I estimated steelhead trout densities within a study reach using the bias-adjusted jackknife estimator as described by Mohr and Hankin in an unpublished manuscript (Hankin 2008, personal communication) and measures of habitat area. Density values were averaged across all sampled habitat units at a site. The number of habitat units sampled varied by site. Biomass values, expressed as g/m^2, were calculated by multiplying the site-specific average weight for juvenile steelhead trout by the average density value for the site. Rather than estimate density based on all steelhead trout for sites outside of cutthroat range and greater than or equal to 70 mm at sites within cutthroat range, biomass values only included steelhead trout greater than or equal to 70 mm.

Turbidity and water temperature data were obtained from multiple agencies that operated automated gauges on the streams sampled. Gauges differed in the length of time they operated in streams and they measured turbidity at different sampling intervals (10 or 15 minutes, Table 4). Two types of gauges were used at the various sample sites, DTS-12 and OBS-3 sensors. The DTS-12 gauge collected temperature in addition to turbidity. For Prairie Creek, where an OBS-3 sensor was used, temperature was collected from a DTS-12 sensor approximately 1.6 km upstream of the site used for this study. For Elder Creek in water year 2006, when the DTS-12 gauge was not operating correctly, temperature data were obtained as daily averages collected from an area 2.2 km upstream of the turbidity and fish sampling site with a HOBO data logger.

The period that all gauges were operational for both 2005 and 2006 was February 11 – April 18. Measures of temperature and turbidity were calculated for this time period for all gauges for both sampling years.

Continuous turbidity values were reported as the percentage of time turbidity exceeded 30 nephelometric turbidity units (NTU). Thirty NTU was on the high end of the range of turbidity levels in the literature that decrease the reactive distance for juvenile *Oncorhynchus mykiss* and other salmonids (Berg and Northcote 1985, Barrett et al. 1992, Gregory and Northcote 1993, Sweka and Hartman 2001b).

Table 4. Turbidity and temperature gauge types, sampling intervals, operating agencies, and percent of turbidity data that was estimated for each site.

Site Name	Turbidity and Temperature Gauge Type	Sampling Interval (min)	Turbidity Gauge Operated by	Percent of Turbidity Data Estimated (%)
2005				
Bull	DTS-12	10	USFS- Redwood Sciences Laboratory	0
Cañon- Lower	DTS-12	10	Green Diamond Resource Company	0
Cañon- Upper	DTS-12	10	Green Diamond Resource Company	0
Carneros	DTS-12	10	Napa Resource Conservation District	4
Cuneo	DTS-12	10	USFS- Redwood Sciences Laboratory	1
Elder	DTS-12	10	USFS- Redwood Sciences Laboratory	N/A [a]
Lost Man	DTS-12	10	USGS	25
Maple- Lower	DTS-12	10	Green Diamond Resource Company	5
Maple- Upper	DTS-12	10	Green Diamond Resource Company	0
Prairie	OBS-3	10	USGS	95 [b]
2006				
Bull	DTS-12	15	USFS- Redwood Sciences Laboratory	4
Elder	DTS-12 [c]	15 [d]	USFS- Redwood Sciences Laboratory	100
Jacoby	DTS-12	10	Randy Klein (hydrologist)	N/A [a]
North Fork Caspar	DTS-12	10	USFS- Redwood Sciences Laboratory	0
South Fork Caspar	DTS-12	10	USFS- Redwood Sciences Laboratory	4

[a] Data were reviewed and any missing readings were interpolated before I received them; there was no notation indicating percent of data estimated.
[b] Turbidity readings corrected by USGS; raw turbidities were higher than the corrected values for 95% of the sampling period.
[c] Turbidities from Elder Creek for 2006 were only for a 2 week period due to malfunctioning of the turbidity gauge. Turbidity values for this sample were estimated using discharge values for 2006 and a discharge-turbidity relationship based on 2007 data. Temperature values were taken as daily averages from an area 2.2 km upstream of the fish sampling site using a HOBO instrument.
[d] Discharge readings which Elder 2006 turbidities were based on were taken every 15 minutes.

Turbidity was also reported as a cumulative value to determine if the magnitude of turbidity readings had a stronger correlation to relative weight than the time a threshold was exceeded. Newcombe and MacDonald (1991) recommended that duration of exposure multiplied by sediment concentration was a better indicator of ill effects of sediment than concentration alone. As such, cumulative turbidity reflects the sediment concentration and also the duration of exposure. Daily averages of turbidity were calculated and summed to determine the cumulative turbidity value. Daily averages were used to normalize data from gauges set to record at different time intervals. Most of the turbidity gauges reached the maximum turbidity value detectable by the gauge at some point over the sampling period. In such cases, the maximum detectable value was used in calculating the daily average turbidity value and any deviations from the true turbidity value were considered negligible.

Each agency had different quality assurance protocols for ensuring reliability of data. Quality assurance methods were reviewed from all agencies to ensure the data used in the analysis were congruent and corrected using similar methods. In general, data were compared to field notes describing gauge status (e.g. gauge out of water or under repairs) and grab samples to ensure the accuracy of the turbidity readings.

In some cases, it was necessary to interpolate missing turbidity or temperature values (Table 4). Supporting data such as stage height, field notes, temperatures from nearby sites, or discharge and turbidity data from other years for the system were used when available in interpolating missing data. The 2005 Elder Creek and Jacoby Creek turbidity and temperature data were reviewed and corrected before I received them and no notation was included indicating what proportion of the data was estimated. The entire 2006 Elder Creek sample was estimated from 2007 discharge and turbidity data ($R^2 = 0.23$) and 2006 discharge data. The average proportion of data that was estimated for all sites was 18%.

Full models with temperature, biomass and a turbidity parameter, were analyzed using the backwards elimination procedure (Zar 1999). Non-significant parameters were removed until only significant parameters remained. For the backwards elimination process, models were evaluated on the significance of the parameter coefficients, based on a 2-tailed t test ($H_O : \beta_i = 0$, Zar 1999).

Average relative weight for each stream was the response variable. The empirical method of standard weight equation better represented the length-weight data based on tests of length bias and comparisons of relative weights derived using the two equations, so that method was used to estimate the average relative weight for each study population.

The two turbidity metrics were analyzed to determine if they exhibited collinearity, since they are different representations of the same turbidity data. Such a condition could result in correlated variables appearing to have significant coefficients when in fact they do not (Zar 1999). The cumulative turbidity measure and the percentage of time over 30 NTU were correlated, as indicated by a high value of r (the correlation coefficient). Since the metrics were highly correlated, they were not used in the same models. Separate full models with temperature, biomass, and each of the turbidity metrics were evaluated using backwards elimination. All combinations of independent variables were plotted against each other and plots were visually inspected to ensure that none of the pairs besides turbidity exhibit collinearity before including them in the full model.

RESULTS

Standard Weight Equations

Of the 100 populations included in the developmental dataset, 41 included information on sampling dates. All months except December were represented in the length-weight data. For the sites where sampling dates were not reported, correspondence indicated they were single sampling events, not recurring samplings of a site. Agencies sampled steelhead trout using backpack electrofishers, downstream traps and seines. Most downstream traps were set for multiple months, but it is unlikely that they represent fish captured more than once. However, one trap (Northspur of the Noyo River, California) was downstream from two other trap sites, and may replicate data from the upstream datasets (Redwood and Olds Creeks, both Noyo tributaries). Seining took place on the West Fork of the Smith River in Oregon from August to November and potentially represent multiple length-weight entries for fish, but it is not possible to be certain.

Using the Flammang et al. (1999) technique, the length range determined for the standard weight equation for juvenile steelhead trout was 50-200 mm. Variance of $\log_{10}$ transformed weights stabilized within this range (Figure 1). Equations were created for both 50-200 mm and 70-200 mm using the empirical equation to ensure there were not significant differences between these two equations. Comparing plots of the relative margin of error ($((2*SE)/mean)*100$) as estimated from bootstrapped samples, values across length were very similar for lengths of 70 – 140 mm for both potential

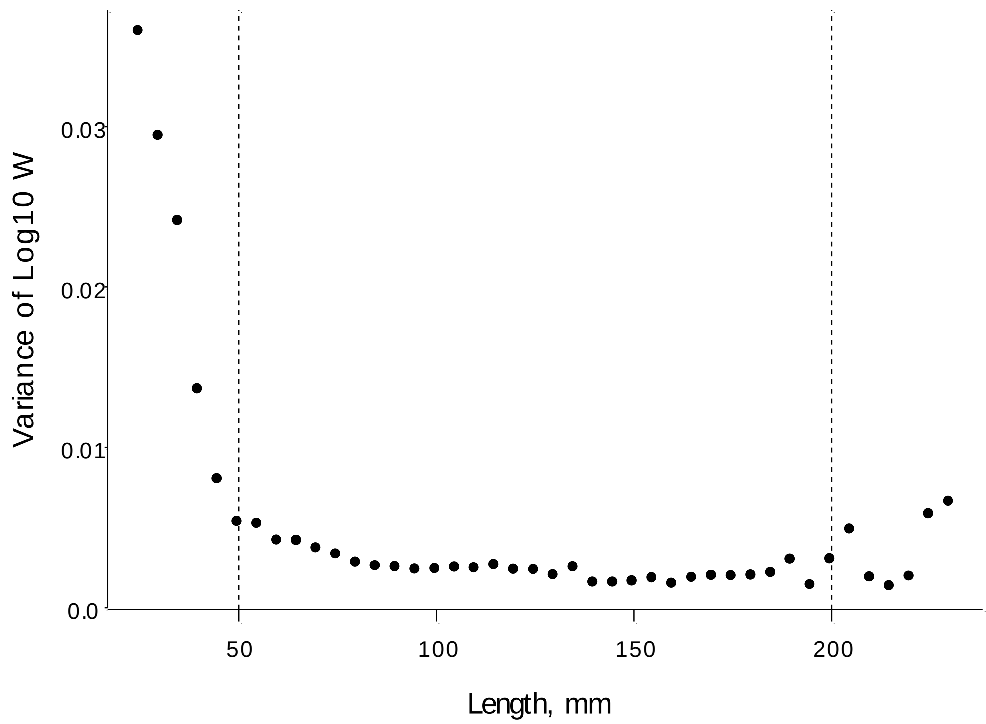

Figure 1. Variance of $\log_{10}$-transformed weights versus length for all juvenile steelhead trout length-weight pairs considered for the standard weight equation developmental dataset.

length ranges (Figure 2). Values for the 70-200 mm equation reach a maximum relative margin of error of 3.47% while values for the 50-200 mm equation peak at 2.30% for the upper end of the length range. Given the difficulty in differentiating between cutthroat and steelhead trout less than 70 mm in length, the length range selected for the standard weight equation was 70-200 mm.

Several populations seemed to be outliers when their intercepts were plotted against slopes of regressions of the $\log_{10}$ weight versus $\log_{10}$ length (Figure 3), and also in the boxplot analysis. These datasets were examined and not found to have any apparent transcription errors to explain why they were outliers. Variation was attributed to environmental differences and the populations were kept in the developmental dataset.

The equation derived using the regression line percentile technique was:

$$\log_{10} W_S = -4.753 + (2.908 * \log_{10} L).$$

The empirical technique resulted in the equation:

$$\log_{10} W_S = -3.497 + (1.659 * \log_{10} L) + \left(0.307 * (\log_{10} L)^2\right).$$

When the standardized residuals of the empirical equation were plotted against length (Figure 4), residuals were grouped around 1 (r = -0.10) and showed no tendency to be above or below 1, suggesting that the equation was not length biased. A similar plot for the regression line percentile equation showed a loose correlation with length (r = 0.41). Values at the low end of the length range had residuals below one. Residual values for the regression line percentile equation increased with increasing length.

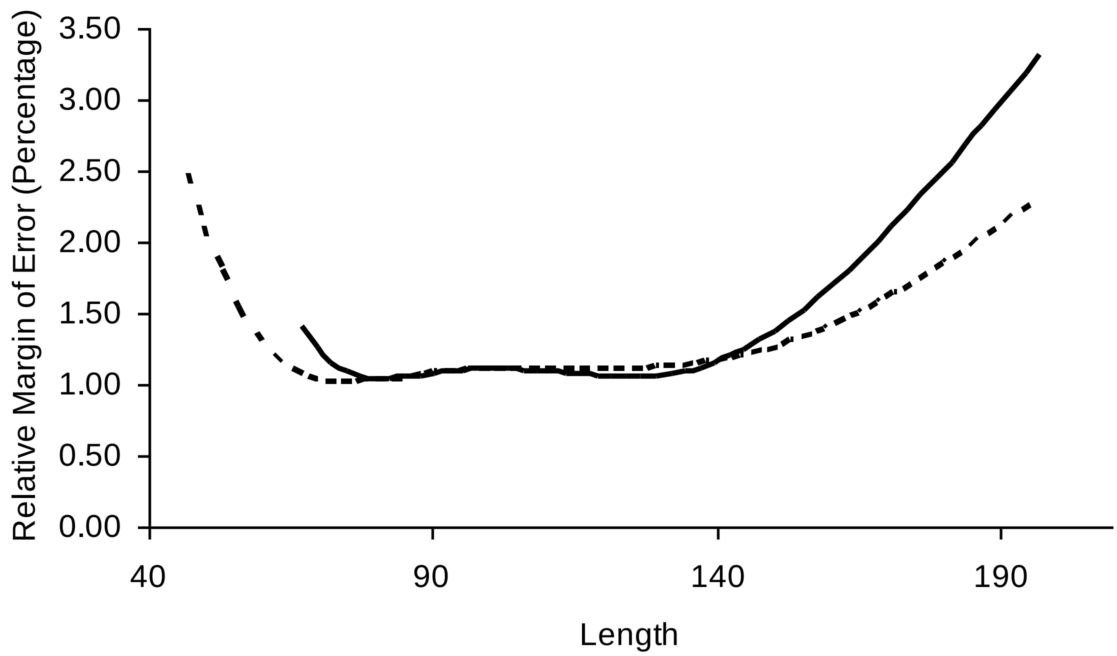

Figure 2. Comparison of relative margin of error plots for the 50-200 mm (dashed line) and 70-200 mm (solid line) empirical standard weight equations for juvenile steelhead trout.

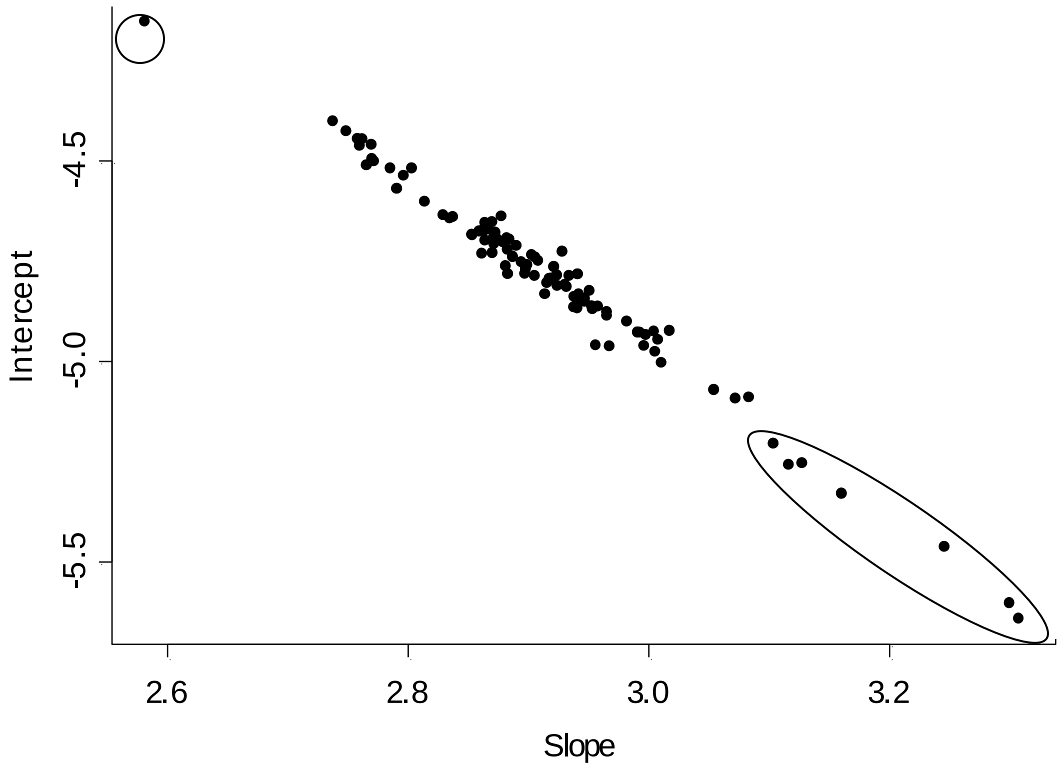

Figure 3. Intercept coefficients versus slope coefficients of log_{10} transformed weight versus length from juvenile steelhead trout populations in the developmental dataset. Eight populations identified as statistical outliers are circled. Data from these populations were included in the developmental dataset as no transcription or measurement errors could be detected.

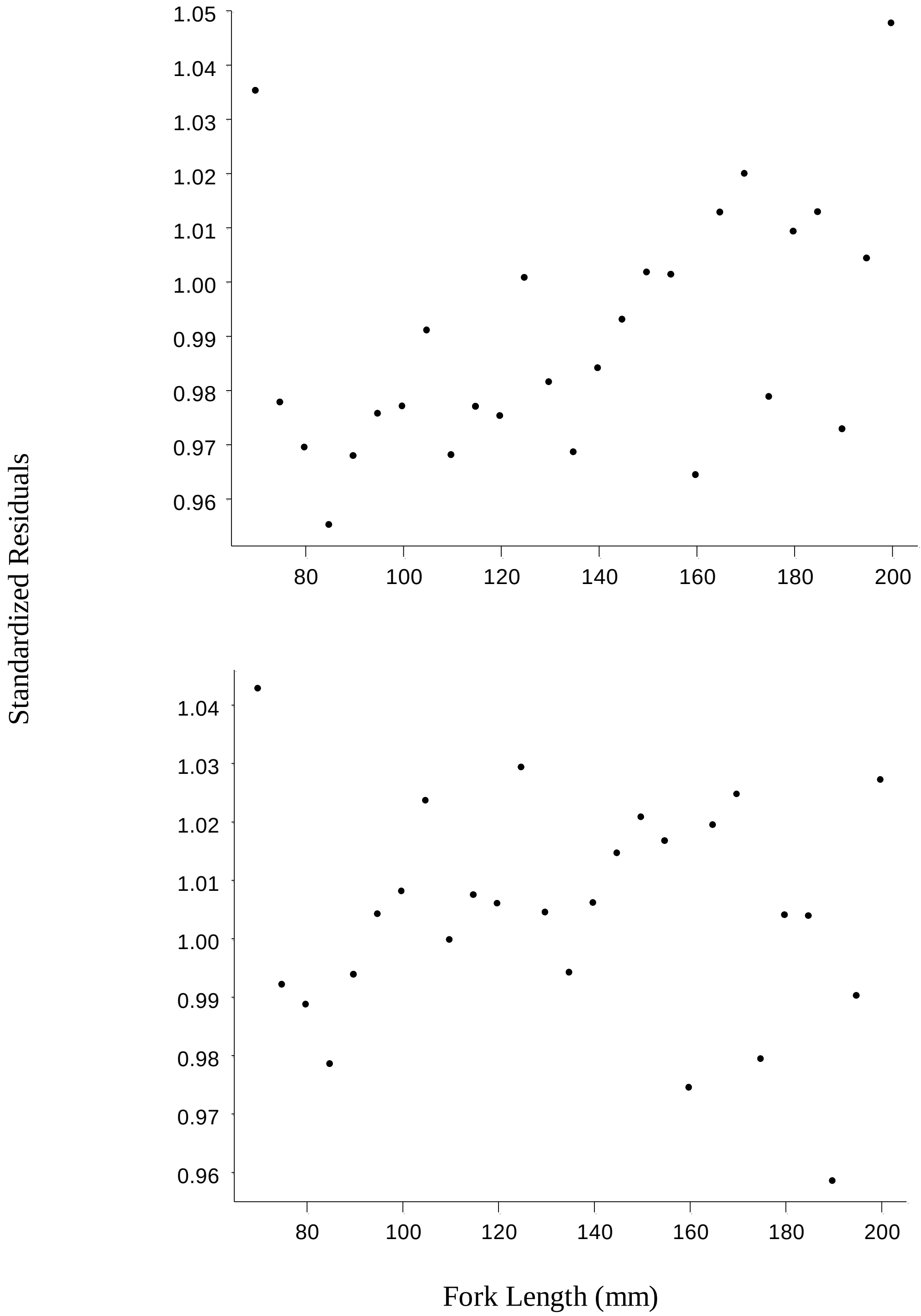

Figure 4. Standardized residuals versus fork length for the regression line percentile (top panel) and empirical (bottom panel) standard weight equations for juvenile steelhead trout.

The empirical quartiles method for length bias (Gerow et al. 2004) produced the weighted quadratic equation:

$$\textit{Standardized Third Quartile} = 106.4 - (0.1549 * L) + (0.0007 * L^2)$$

(R^2 =0.24, p-value = 0.0392). The significance of the quadratic regression suggests that the regression line percentile standard weight equation may repress natural curvature in the length weight data.

Further support for the use of the empirical form of the standard weight equation comes from the comparison of relative weights estimated using the regression line percentile and empirical equations (Gerow et al. 2005). The regression line percentile and empirical relative weight values differed slightly over the length ranges of the equations (Figure 5, the maximum difference was 3.2).

Given the better fit of a quadratic regression to the length-weight data, the empirical version of the standard weight equation was used to estimate relative weights for my study populations. The empirical quartiles length bias output, the differences in regression line percentile and empirical relative weights over the length range, and the recommendations in the literature to use the empirical form of standard weight equations (Gerow et al. 2005, Richter 2007) further support the use of the empirical equation.

Biomass and Relative Weight

Numbers of steelhead trout greater than 70 mm varied from 0.02 fish/m^2 on Prairie Creek to 0.44 fish/m^2 on the lower site of Cañon Creek. Estimated biomass

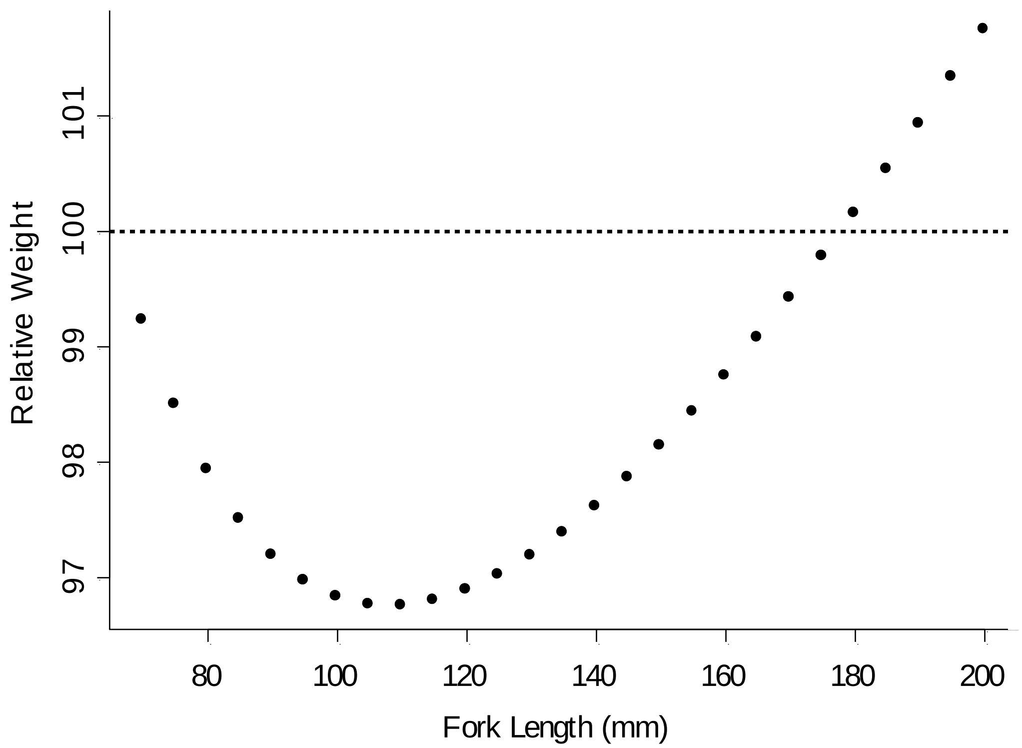

Figure 5. Relative weight values estimated using the regression line percentile and empirical techniques plotted against fork length (mm) for juvenile steelhead trout. Weights representing empirical relative weights of 100 are indicated by the dotted line; the equivalent regression line percentile relative weights are indicated by the closed circles.

values were lowest for Prairie Creek (0.19 g/m^2) and highest for Cuneo Creek (3.68 g/m^2). The average estimated biomass for all sites was 1.46 g/m^2.

Average relative weight values differed among sites. Elder Creek (2006) had the lowest average relative weight value (96.5) and Carneros Creek (2005) had the highest (110.3). The average relative weight across sites was 100.5. See Table 5 for a full list of steelhead trout abundance, estimates of biomass, and average relative weight for study sites.

Turbidity and Temperature

Temperature and turbidity values varied over the sample sites for the period of February 11 – April 18. Multiple sites had turbidity readings at or near the minimum (0 NTU) and maximum (approximately 1600 NTU) detectable by the turbidity gauges. Average turbidity for all sites was 40 NTU. The lowest temperature was observed on South Fork Caspar Creek (2.2 ºC) while Carneros Creek had the highest reading (16.1 ºC). Temperature averaged 9.1 ºC across all the sites.

Percentage of time that turbidity exceeded 30 NTU ranged from 0% on Elder Creek (2005) to 66% on Bull Creek in 2006 (Table 5). Elder Creek also had the lowest cumulative turbidity during 2005 (119 NTU) and Bull Creek had the highest in 2006 (7419 NTU). Turbidity values for Bull Creek and Elder Creek varied between 2005 and 2006. Cumulative turbidity on Bull Creek ranged from 4108 in 2005 to 7419 in 2006. On Elder Creek, the cumulative turbidity value in 2005 was 119 and the estimated value in 2006 was 2371.

Table 5. Characteristics of juvenile steelhead trout populations, and temperature and turbidity data from Northern California streams. Turbidity and temperature values summarize data from February 11 – April 18 of each year, prior to fall fish sampling. Relative weight (W_r) values are the average for all juvenile steelhead trout between 70 – 200 mm calculated using the empirical method.

Site Name	# of steelhead trout ≥ 70 mm	Average empirical W_r	Biomass (g/m^2)	Time turbidity exceeds 30 NTU[a] (%)	Cumulative turbidity	Temperature (degree days)
2005						
Bull	192	105.3	1.47	45.56	4108	680.8
Cañon- Lower	314	100.8	2.98	28.62	2885	604.1
Cañon- Upper	113	100.7	1.33	23.24	2123	607.2
Carneros	204	110.3	0.33	29.41	3543	784.8
Cuneo	134	104.9	3.68	39.55	6420	663.5
Elder	53	99.6	1.92	0.16	119	592.5
Lost Man	67	99.4	0.37	8.83	971	648.4
Maple-Lower	110	97.9	2.21	38.18	3112	542.0
Maple- Upper	126	96.6	2.65	17.00	1718	532.1
Prairie	33	102.7	0.19	4.88	416	604.7[b]
2006						
Bull	179	101.3	1.82	65.53	7419	593.7
Elder	84	96.5	1.03	13.20[c]	2371[c]	544.9[d]
Jacoby	118	100.2	0.68	30.22	1939	538.3
North Fork Caspar	20	98.8	0.25	26.96	1957	618.2
South Fork Caspar	34	96.7	0.53	53.14	2580	593.7

[a] NTU = Nephelometric Turbidity Units.
[b] Temperature readings taken approximately 1 mile upstream of turbidity gauge.
[c] Turbidity predicted using discharge readings and a relationship between turbidity and discharge from 2007 data.
[d] Temperature data from a site approximately 1 mile upstream of the turbidity gauge.

The percentage of time turbidity exceeded 30 NTU showed similar variability for Bull and Elder Creeks between 2005 and 2006 (Table 5). Across sample sites, cumulative turbidity averaged 2652 and percentage of time turbidity exceeded 30 NTU averaged 28.

Values for degree days ranged from 532 degrees days for the upper site on Maple Creek to 785 degrees days for Carneros Creek. Temperature values between years on Bull Creek and Elder Creek did not vary greatly (Table 5). The average temperature in degree days across the sites was 610.

Models

The two turbidity metrics, percentage of time above 30 NTU and cumulative turbidity, were highly correlated, as indicated by a correlation coefficient of 0.83. None of the other independent variables showed a strong level of correlation, judging from plots of the variables (Figure 6).

Both full models had high adjusted R^2 values and both had variables that were not significant (Tables 6, 7). The biomass and turbidity parameters (percentage of time over 30 NTU and cumulative turbidity) had high p-values and were not significant. Backwards elimination for both full models resulted in a model with only the temperature parameter, which was significant at the 0.05 level. The model is valid for degree days from 532 – 785 based on temperature readings from 2.2 to 16.1º C. Figure 7 includes a plot of average relative weight versus temperature in degree days and the fitted regression line.

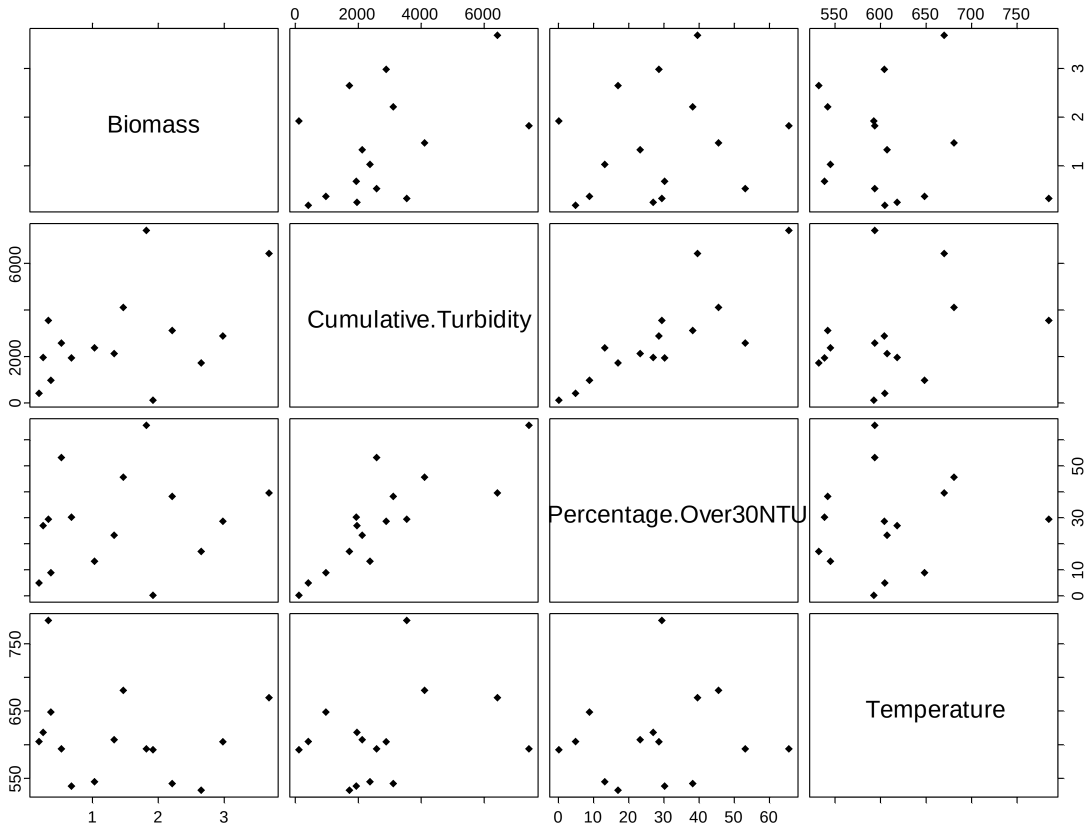

Figure 6. Plot of all combinations of independent variables (n = 15). Two sites (Bull Creek and Elder Creek) were sampled in 2005 and 2006 and treated as independent samples. Note the high correlation between the Cumulative Turbidity and Percentage Over 30 NTU variables.

Table 6. Estimated coefficients for models in the backwards elimination procedure for models containing the percentage of time over 30 Nephelometric Turbidity Units (NTU) variable (n = 15). Response variable is average relative weight estimated using the empirical method for juvenile steelhead trout between 70 – 200 mm. Temperature expressed as degree days over February 11 – April 18.

Model parameters	Coefficient value	Standard Error	t-value	Pr(>|t|)	Adjusted R^2
Intercept	68.67	5.23	13.12	0.00	
Biomass	0.47	0.51	0.93	0.37	0.72
Temperature	0.05	0.01	6.14	0.00	
Percentage Over 30 NTU	0.01	0.03	0.21	0.84	
Intercept	68.65	5.02	13.67	0.00	
Biomass	0.50	0.48	1.04	0.32	0.74
Temperature	0.05	0.01	6.52	0.00	
Intercept	70.30	4.78	14.71	0.00	0.74
Temperature	0.05	0.01	6.41	0.00	

Table 7. Estimated coefficients for models in the backwards elimination procedure for models containing the cumulative turbidity variable (n = 15). Response variable is average relative weight for a site estimated using the empirical method for juvenile steelhead trout between 70 – 200 mm. Temperature expressed as degree days.

Model parameters	Coefficient value	Standard Error	t-value	Pr(>|t|)	Adjusted R^2
Intercept	69.79	5.40	12.93	0.00	0.73
Biomass	0.29	0.57	0.50	0.63	
Temperature	0.05	0.01	5.59	0.00	
Cumulative Turbidity	0.00	0.00	0.69	0.51	
Intercept	71.92	4.75	14.94	0.00	0.74
Temperature	0.05	0.01	5.97	0.00	
Cumulative Turbidity	0.00	0.00	1.16	0.27	
Intercept	70.30	4.78	14.71	0.00	0.74
Temperature	0.05	0.01	6.41	0.00	

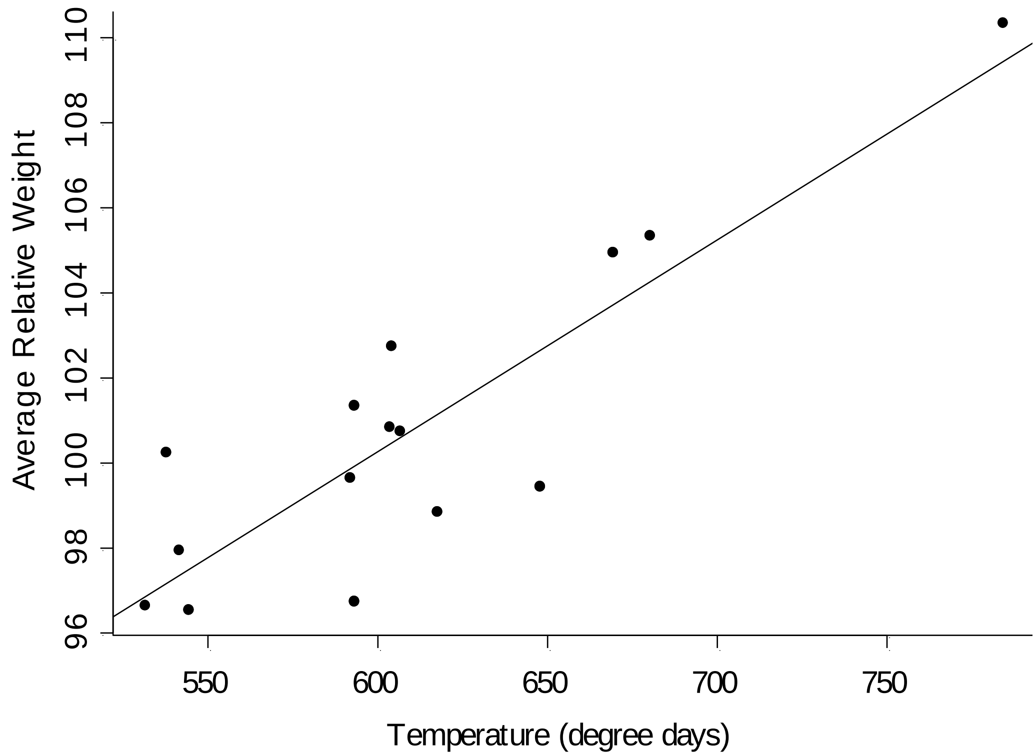

Figure 7. Average relative weight versus temperature across study sites (n = 15). Regression line represents the model estimated using backwards elimination analysis. The model was based on temperature ranging from 532 – 785 degree days from temperature readings from 2.2 to 16.1º C.

DISCUSSION

The empirical method (Gerow et al. 2005) resulted in a standard weight equation that appears to be both representative of the juvenile steelhead trout lengths and weights in the developmental dataset and free from length bias. The empirical quartiles method to test for length bias resulted in a quadratic regression with a low p-value. This suggests that a quadratic equation was a more accurate expression of the juvenile steelhead trout length-weight data than the linear equation used in the regression line percentile method (Gerow et al. 2004). The curvature exhibited by regression line percentile values in the comparison of regression line percentile and empirical relative weights (Figure 5) was likely an artifact of the two equations being different forms (linear versus quadratic).

Another reason not to use the regression line percentile equation concerns methodology. In Springer et al. (1990), Cone suggested that the regression line percentile technique is "statistically questionable". The regressions that constitute the statistical population modeled for the regression line percentile standard weight equation are sometimes extrapolated beyond the lengths represented in the empirical data. This issue is addressed in the empirical method since empirical lengths and weights from populations in the developmental dataset are used to develop the standard weight equation directly.

The possibility that more than one length-weight pair per fish was included in the developmental dataset (from the Noyo River or the West Fork of Smith River) is not ideal. The length-weight pairs from these two populations represent 3.5% of the 23,007 pairs included in the developmental dataset. Given this small proportion and the possibility that data from these populations were not duplicates, the impact of potentially re-sampled fish on the standard equation is likely negligible.

Future attempts at developing standard weight equations using the empirical method should perhaps consider relative margin of error results from bootstrap iterations in the selection of length limits for the equation. In my study, I used the published method for determining length limits (Flammang et al. 1999). However in comparing output from 50 – 200 mm and 70 – 200 mm equations (Figure 2), I looked at relative margin of error of median standard weight estimates. For both proposed length ranges, the relative margin of error increased starting at length of approximately 140 mm. Future studies should determine if there is an upper allowable limit for the error estimates, causing lengths with errors beyond this upper cutoff to be outside the length range. Another possibility would be to determine the length range based on the length at which relative margin of error increases.

In my study, the relative weight of juvenile steelhead trout populations in northern California during fall was positively related to degree day accumulation during the previous early-spring period. A laboratory study of age-0 steelhead trout similarly observed increased growth rates at increasing temperatures up to 19º C (Myrick and Cech 2005). Using bioenergetics modeling, Railsback and Rose (1999) found that high fall-spring temperatures (reaching a maximum of approximately 11º C) resulted in increased simulated growth in juvenile rainbow trout.

It should be noted that summer temperatures in excess of a maximum threshold (maximum weekly average temperature of 17º C) have been linked to a decrease in juvenile rainbow trout growth (Nelitz et al. 2007). In my study, the increase in average relative weights was related to degree days from 532 – 785, based on temperature readings from 2.2 to 16.1ºC. The model describing the positive relationship of average relative weight and temperature is only applicable to this range of temperature data. The effect of temperature on relative weight should be further explored to see if relative weight decreases beyond some upper temperature threshold. As maximum temperatures are often of interest in studies related to restorations (e.g. Nelitz et al. 2007), exploring the effects of a broader range of temperatures on relative weight would make this metric more relevant in describing the impacts of habitat restorations on juvenile steelhead trout.

Neither steelhead trout biomass nor turbidity were shown to have a significant relationship with relative weight. Previous research on salmonids has shown both variables have an inverse relationship with weight or growth (for density: Wentworth and LaBar 1984, Close and Anderson 1992, Keeley 2003; for turbidity: Sweka and Hartman 2001a). It is possible that biomass and turbidity do indeed have an effect on fish size, but that the average relative weight metric used in this study does not accurately represent the relationship. Length may be a more appropriate measure of size, as seen in Hunt's (1969) study showing a decrease in length with increasing fish density in brook trout. Another possibility is the standard deviation of relative weight may be a more appropriate metric. Wege and Anderson (1978) found an inverse relationship between the standard deviation of largemouth bass relative weight and fish density, hypothesizing that as density increased, feeding rate became uniform.

It is possible that any decrease in condition caused by turbidity was recovered in the time between elevated turbidity and fish sampling. Recovery of weight lost over winter was seen in 0+ Atlantic salmon, which, by early April, fully recovered weight lost during October through January (Egglishaw and Shackley 1977). For my study, I sampled 4 sites in June in an attempt to estimate relative weights closer to turbidity events. However the small sample size made the data inconclusive.

Alternatively, models in this study could be correct in indicating that turbidity does not have a negative effect on condition. A number of studies of salmon have shown fish to be unaffected by high levels of turbidity. In a laboratory study of juvenile rainbow trout, feeding rates did not decrease for increases in turbidity up to 160 NTU, the highest turbidity level studied (Rowe et al. 2003). James and Graynoth (2002) found the mean weights and condition factors of rainbow trout in lakes were not significantly affected by water clarity levels. White and Harvey (2007) found that feeding success in rainbow trout in northern California was not significantly affected by periods of high flow and turbidity. Similarly, a recent laboratory study also showed that juvenile salmon were able to feed from the benthos in turbid (up to 150 NTU) conditions (Harvey and White 2008).

Biomass may not have had a significant relationship to relative weight because this study only looked at biomass of juvenile steelhead trout greater than or equal to 70 mm. It is possible that steelhead trout less than 70 mm or other salmonids competed for prey and could have influenced relative weight of the fish in our study, as seen in a study by Young (2004) that showed coho salmon could successfully compete with steelhead trout. In the sites that I sampled, the proportion of steelhead trout greater than or equal to

70 mm compared to all salmonids (including steelhead trout less than 70 mm) varied from 6.6% on Prairie Creek to 98.6% on Carneros Creek. This large variation among sites indicates that inclusion of all salmonids in a biomass estimate should be considered in future analyses of density effects on relative weight.

Another potential explanation for not detecting a relationship between condition and biomass is that food may not have been limiting. Future studies should try to explore condition in streams that are known to have high biomass levels resulting in density-dependent effects on growth or size.

It should be noted that DeYoung (2007) studied Cañon and Maple Creeks and found that fish moved within the upstream and downstream sites on these two streams. Fish sampled from these 4 sites may not reflect the turbidities they were associated with in my analysis. This also raises the question of whether any of the reported turbidities were accurate descriptions of the turbidity that the juvenile steelhead trout I sampled were exposed to. While turbidities were likely approximations of the conditions experienced by steelhead trout, future studies should avoid using multiple turbidity sampling sites on a stream or ensure they are far enough apart to prohibit significant movement between them.

Average relative weights for populations that I sampled ranged from 96.5 – 110.3 and average relative weight across my sites was 100.8. The range of average relative weight for populations in my developmental dataset ranged from 78.2 to 118.1 with an average of 97.7. Comparing these values shows that populations that I sampled in northern California are not representative of as wide a range of average relative weight values as the populations in the developmental dataset. This limited range of relative weights may have prevented the detection of trends in condition and environmental or population variables.

Another source of error was measurement error. A subsample of 12 fish from Bull Creek was weighed twice during the 2006 sample. The weights were measured on different electronic balances (Table 8), and the difference in measurements, though small, was enough to cause a difference in average relative weight for the two groups of weights (104.18 versus 101.43). Since the range of average relative weights across samples was not great in this study, such a difference in measured weight could affect the significance of the models under consideration.

I was unable to determine if the lack of relationship between relative weight and turbidity and biomass is a true reflection of the relationship or a fault of the condition index used in this study. Several studies using the regression line percentile method found no connection with relative weight and lipid reserves (Simpkins et al. 2003), growth (Gutreuter and Childress 1990), food (Hartman and Margraf 2006), or numerous physical and chemical characteristics and fish density and biomass (Austen et al.1994). There are not yet enough studies using the empirical method to determine patterns in the utility of condition estimated using this method. Rennie and Verdon (2008) evaluated regression line percentile- and empirical-derived standard weights for lake whitefish found that regression line percentile-derived values were more strongly correlated with physiological condition indices. Further studies on the empirical standard weight

Table 8. Comparison of weights (W) and relative weights (W_r) from different electrical balances for a subsample of fish from Bull Creek 2006. W_r values were estimated using the empirical standard weight equation for juvenile steelhead trout.

Length	W from balance #1	W from balance #2	W_r calculated from balance #1 weight	W_r calculated from balance #2 weight
76	5.82	5.76	113.7	112.5
83	7.15	6.95	108.9	105.8
101	11.44	11.35	99.3	98.5
78	6.14	5.85	111.5	106.2
84	7.10	7.04	104.5	103.6
81	5.92	5.62	96.6	91.7
73	4.85	4.47	106.1	97.8
72	4.59	4.49	104.3	102.1
79	5.72	5.63	100.2	98.6
82	6.83	6.59	107.6	103.9
89	8.08	8.02	100.9	100.1
88	7.50	7.48	96.7	96.4
		Average W_r	104.2	101.4

equation should be conducted to determine if this metric is consistently linked to physiological condition, and population and environmental variables.

Although temperature was the only variable in this study shown to have a significant effect on relative weight values, it is likely that other habitat and population variables affect relative weight. Previous studies have found relationships between relative weight and food supply (Flickinger and Bulow 1993, Liao et al. 1995), season (Fechhelm et al. 1995), and habitat characteristics (small versus large impoundments, Guy and Willis 1995; lentic versus lotic systems, Fisher et al. 1996). Considering the diversity of variables correlated with relative weight, a model with only one parameter cannot capture the complexity of relationships and interactions of all variables that have been related to condition.

The need for models that capture the effects of numerous variables that affect size is illustrated in this study by the minimum and maximum average relative weights observed across my sample sites. The lowest relative weight value was estimated for steelhead trout on Elder Creek in 2006 (96.5) while the highest average was on Carneros Creek in 2005 (110.3). While these sites differed in temperatures over February 11 – April 18, there was variation in other habitat and population measures that were not captured by the parameters considered in this study. For example, land use differed between the two sites: Elder Creek is managed as a nature reserve while Carneros Creek runs through a vineyard. The sites also differed in amount of habitat available to juvenile steelhead trout. For the 200 m reach surrounding the turbidity gauge, Elder Creek had a surface area of 1214 m^2 while a similar length of stream on Carneros Creek only had a surface area of 598 m^2. The extent of vegetation along the streams also varied. Elder Creek ran through a forest, while Carneros Creek was bordered by a narrow strip of trees. It seems unlikely that the relationship between average relative weight and fall-spring temperature illustrates these differences in habitat.

Additional studies to understand how relative weight estimated using the empirical method relates to habitat quality, and measures of population and growth are necessary before using relative weight as a metric to track habitat effects. If relative weight is in fact shown to have strong relationships with steelhead trout physiology and environmental variables, other population metrics (e.g. length, growth, density) should still be taken into consideration when making management decisions (Hansen and Nate 2005) in order to best describe the impact of habitat on steelhead trout size and productivity.

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Appendix A. Information on populations of juvenile steelhead trout in the developmental dataset, including agency that contributed data, location, sample size, and regression parameters and correlation (R^2) of $\log_{10}$ transformed weight and length. Average relative weight (W_r) was estimated using the empirical standard weight equation.

Stream	State	Contributing Agency[a]	Sample size	Slope	Intercept	R^2	Average W_r
Bozo Creek	AK	USFS	41	3.247	-5.467	0.94	88.9
Cable Creek	AK	USFS	141	2.917	-4.809	0.97	94.6
Falls Creek	AK	USFS	66	3.007	-4.980	0.96	96.7
Fowler Creek	AK	USFS	97	2.939	-4.870	0.95	90.0
Kadashan River	AK	USFS	45	3.118	-5.263	0.98	83.4
Maybeso Creek	AK	USFS	358	2.942	-4.866	0.98	92.7
Pile Driver	AK	USFS	93	3.012	-5.009	0.94	89.3
Saginaw Creek	AK	USFS	92	3.129	-5.258	0.98	86.2
Sal River	AK	USFS	70	2.883	-4.767	0.99	88.8
Snipe Creek	AK	USFS	41	2.942	-4.872	0.96	91.9
South Fork Staney River	AK	USFS	91	2.907	-4.791	0.91	92.8
Staney (at Fred's)	AK	USFS	30	2.884	-4.787	0.98	85.2
Staney (at Knob Creek)	AK	USFS	63	2.958	-4.964	0.90	78.2
Staney (at Tye Creek)	AK	USFS	89	3.302	-5.607	0.95	80.7
Staney River	AK	USFS	46	2.863	-4.736	0.98	87.3
West Fork Saginaw	AK	USFS	45	3.105	-5.210	0.98	87.4
Albion River	CA	Mendocino Redwoods Company	58	2.762	-4.467	0.98	102.2
Amaya Creek	CA	NOAA	37	2.750	-4.431	0.98	104.8
Bear Creek (Santa Cruz County)	CA	NOAA	37	2.925	-4.791	1.00	101.2
Bear River	CA	NOAA	47	2.943	-4.787	0.98	111.0
Big Creek	CA	NOAA	57	2.916	-4.836	0.98	87.7
Big Creek (Humboldt County)	CA	NOAA	56	2.936	-4.791	1.00	105.6
Big Creek (Monterey County)	CA	NOAA	92	2.739	-4.406	0.98	105.8
Big Flat	CA	USGS	203	2.855	-4.689	0.98	92.8

[a] NOAA is the Salmon Population and Analysis Team at NOAA Fisheries- Southwest Fisheries Science Center-Santa Cruz Laboratory. USGS is the USGS California Cooperative Fish Research Unit. CDFG is the California Department of Fish and Game- Anadromous Fisheries Resource Assessment and Monitoring Program.

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Stream	State	Contributing Agency[a]	Sample size	Slope	Intercept	R^2	Average W_r
Big River (Gates Creek)	CA	Mendocino Redwoods Company	47	2.881	-4.708	0.99	100.6
Big River (Wildhorse opening)	CA	Mendocino Redwoods Company	41	2.967	-4.882	0.99	97.8
Big Salmon River	CA	NOAA	49	3.019	-4.928	0.90	111.6
Big Sur River	CA	NOAA	46	2.994	-4.933	0.93	98.5
Blue Creek	CA	NOAA	75	2.993	-4.932	0.99	100.3
Boulder Creek	CA	NOAA	43	2.865	-4.677	0.99	100.3
Bridge Creek	CA	Redwood National and State Parks	111	2.933	-4.818	0.99	99.5
Bummer Lake Creek	CA	USGS	126	2.954	-4.867	0.98	97.6
Campbell Creek	CA	NOAA	61	2.930	-4.732	0.99	118.1
Carbonera Creek	CA	NOAA	67	2.953	-4.829	0.98	104.9
Carmel River	CA	NOAA	53	2.771	-4.464	0.98	107.9
Carson Creek	CA	Green Diamond Resource Company	629	2.855	-4.690	0.97	93.9
Caspar Creek	CA	CDFG	182	2.793	-4.574	0.97	90.0
Cheda Creek	CA	Point Reyes National Seashore	93	2.948	-4.856	0.99	96.8
Coyote Creek	CA	Redwood National and State Parks	88	2.884	-4.698	0.99	103.9
Devil's Gulch	CA	Point Reyes National Seashore	257	2.921	-4.798	0.96	98.5
East Fork Mill Creek	CA	USGS	110	2.889	-4.745	0.99	95.7
East Fork North Fork Trinity River	CA	CDFG	187	2.872	-4.734	0.97	91.1
East Fork Soquel	CA	NOAA	216	2.942	-4.847	0.98	96.6
Elk Creek	CA	Mendocino Redwoods Company	51	2.932	-4.814	0.99	99.4
Greenwood Creek	CA	Mendocino Redwoods Company	86	2.881	-4.707	0.99	100.7
Hare Creek	CA	CDFG	102	2.896	-4.757	0.97	96.4
Hayworth Creek	CA	CDFG	157	2.926	-4.816	0.96	96.6

[a] NOAA is the Salmon Population and Analysis Team at NOAA Fisheries- Southwest Fisheries Science Center-Santa Cruz Laboratory. USGS is the USGS California Cooperative Fish Research Unit. CDFG is the California Department of Fish and Game- Anadromous Fisheries Resource Assessment and Monitoring Program.

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Stream	State	Contributing Agency[a]	Sample size	Slope	Intercept	R^2	Average W_r
Horse Linto Creek	CA	NOAA	36	2.901	-4.764	0.99	96.3
John West Fork	CA	Point Reyes National Seashore	89	2.919	-4.799	0.99	96.2
Kass Creek	CA	NOAA	40	2.983	-4.905	0.98	100.5
Kinsey Creek	CA	USGS	76	2.944	-4.838	0.99	99.3
Lagunitas Creek	CA	Marin Municipal Water District	81	2.866	-4.659	0.98	104.9
Lawrence Creek	CA	NOAA	36	2.886	-4.701	0.99	104.4
Little Grass Valley	CA	CDFG	38	3.309	-5.646	0.97	90.3
Little North Fork Noyo River	CA	NOAA	45	2.967	-4.890	0.98	97.0
Los Trancos Creek	CA	NOAA	34	2.787	-4.523	0.99	100.2
Lost Man Creek	CA	Redwood National and State Parks	86	2.760	-4.450	0.98	105.7
Low Divide Creek	CA	USGS	45	3.056	-5.075	0.99	95.5
Lower South Fork Little River	CA	Green Diamond Resource Company	657	2.836	-4.648	0.92	95.4
Mark West Creek	CA	Sonoma County Water Agency	737	2.899	-4.775	0.99	93.9
Miller Creek	CA	NOAA	58	2.798	-4.541	0.98	101.8
Millington Creek	CA	Sonoma County Water Agency	68	2.998	-4.966	0.99	95.4
North Fork Big River	CA	NOAA	30	3.085	-5.094	0.99	103.0
North Fork Noyo River	CA	CDFG	231	2.861	-4.681	0.96	98.4
Northspur Noyo River	CA	CDFG	555	2.940	-4.844	0.95	96.0
Olds Creek	CA	CDFG	124	2.816	-4.606	0.91	95.7
Olema Creek	CA	Point Reyes National Seashore	923	2.839	-4.644	0.99	96.5
Panther Creek	CA	NOAA	34	2.949	-4.848	0.99	99.2
Penington Creek	CA	NOAA	31	3.009	-4.951	0.99	104.7

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Appendix A. Information on populations of juvenile steelhead trout in the developmental dataset, including agency that contributed data, location, sample size, and regression parameters and correlation (R^2) of $\log_{10}$ transformed weight and length. Average relative weight (W_r) was estimated using the empirical standard weight equation (continued).

Stream	State	Contributing Agency [a]	Sample size	Slope	Intercept	R^2	Average W_r
Pine Gulch	CA	Point Reyes National Seashore	461	2.876	-4.700	0.99	100.1
Potato Creek	CA	CDFG	41	2.969	-4.967	0.97	84.0
Prairie Creek	CA	NOAA	46	2.907	-4.745	0.99	103.7
Railroad Creek	CA	Green Diamond Resource Company	636	2.889	-4.743	0.97	96.5
Redwood (Noyo R. tributary)	CA	CDFG	48	2.999	-4.939	0.96	102.4
Redwood Creek (Pt. Reyes)	CA	Point Reyes National Seashore	352	2.884	-4.726	0.99	97.9
Ryan Creek	CA	Green Diamond Resource Company	138	2.872	-4.657	0.98	108.8
San Geronimo Creek	CA	Marin Municipal Water District	70	2.959	-4.867	0.98	100.6
San Pedro Creek	CA	NOAA	38	2.905	-4.739	0.97	104.8
San Simeon Creek	CA	NOAA	61	2.868	-4.675	0.99	102.3
Santa Rosa Creek	CA	Sonoma County Water Agency	717	2.873	-4.712	0.99	96.2
Shasta River	CA	CDFG	440	2.764	-4.450	0.96	96.8
Smith Creek	CA	NOAA	93	2.879	-4.643	0.97	116.2
Soldier Creek	CA	CDFG	51	3.162	-5.335	0.94	88.6
South Fork Bear Creek	CA	USGS	411	2.910	-4.754	0.99	103.5
South Fork Noyo River	CA	NOAA	32	2.873	-4.698	0.97	99.6
South Fork Ten Mile River	CA	NOAA	114	2.874	-4.683	0.97	103.7
Spanish Creek	CA	USGS	217	2.923	-4.769	0.99	106.0
Upper South Fork Little River	CA	Green Diamond Resource Company	1103	2.831	-4.640	0.91	95.0
Waddell Creek	CA	NOAA	88	2.805	-4.523	0.96	110.0
Wages Creek	CA	NOAA	57	2.865	-4.679	0.99	99.6
Walker Creek	CA	NOAA	77	3.006	-4.930	0.99	104.7
West Branch Corralitos Creek	CA	NOAA	38	2.583	-4.157	0.99	91.4

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Stream	State	Contributing Agency [a]	Sample size	Slope	Intercept	R^2	Average W_r
Willow Creek (Monterey County)	CA	NOAA	88	2.773	-4.506	0.97	98.7
Willow Creek (Sonoma County)	CA	NOAA	34	3.074	-5.097	0.99	97.8
Zayante Creek	CA	NOAA	35	2.767	-4.516	0.98	93.5
West Fork Smith River	OR	Oregon Department of Fish and Wildlife	263	2.955	-4.875	0.98	97.3
Asotin Creek	WA	Washington Department of Fish and Wildlife- Asotin Creek Project and Bonneville Power Administration	7755	2.866	-4.703	0.99	94.1
Chiwawa Creek	WA	Washington Department of Fish and Wildlife	109	2.772	-4.500	0.98	91.3
Lower Wenatchee River	WA	Washington Department of Fish and Wildlife	220	2.899	-4.786	0.95	88.7
Tucannon Creek	WA	Washington Department of Fish and Wildlife	248	2.892	-4.716	0.96	104.6

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