Polymorphic mountain whitefish (*Prosopium williamsoni*) in a coastal riverscape: Size class assemblages, distribution, and habitat associations

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Abstract

Polymorphic mountain whitefish (*Prosopium williamsoni*) in a coastal riverscape: Size class assemblages, distribution, and habitat associations

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Fluvial mountain whitefish (*Prosopium williamsoni*) offer a rare example of trophic polymorphism among stream dwelling salmonids in temperate North American river systems. Trophic polymorphism is a form of resource-based phenotypic diversification that occurs when exploitation of under-utilized resources necessitates specific morphological characteristics. Studies of trophic polymorphism in the species are few, focusing on diet, foraging behavior, genetic variation, and snout morphology. Pinocchio whitefish develop an elongated snout used to overturn substrate while foraging for benthic invertebrates, whereas normal whitefish have an even sloping head shape and feed primarily on drifting prey. I hypothesized that (1) morphotypes would be associated with distinctly different habitat features based on known feeding behavior and diet, and (2) these differences in habitat association would segregate morphotypes at channel unit and reach scales. In this study, I first compared the spatial distributions of morphotypes and size classes. I then assessed the assemblage structure of morphotypes and size classes and their relationships with aquatic habitat. Finally, I quantified the associations between specific morphotypes and longitudinal variation in aquatic habitat. Spatially continuous sampling was conducted over a broad extent (29 km) in the Calawah River, WA (USA). Whitefish were enumerated via snorkeling in three size classes: small (10-29 cm), medium (30-49 cm), and large (≥ 50 cm). Spatial distributions were compared among size classes of morphotypes by relating cumulative abundance to distance upstream. Assemblage structure and relationships with aquatic habitat were assessed with non-metric multidimensional scaling (NMS). Unit-scale differences between morphotypes in pool and non-pool habitats were quantified with Wilcoxon rank sum tests. Associations between specific morphotypes and habitat were quantified at the 1-km reach scale with generalized additive models (GAMs) using thin-plate regression splines. Large size classes of both morphotypes were distributed downstream of small and medium size classes, and normal whitefish were distributed downstream of pinocchio whitefish. Normal whitefish size classes were associated with higher gradient and depth, whereas pinocchio whitefish size classes were positively associated with pool area, distance upstream, and depth. Normal whitefish relative density did not differ between habitat types at the unit scale ($p = 0.34$, $W = 3085$), but pinocchio whitefish were more dense in pool habitat than in non-pool habitat ($p < 0.0001$, $W = 1084$). Reach-scale GAMs indicated that normal whitefish were associated with larger substrate size in downstream reaches ($R^2 = 0.64$), and pinocchio whitefish were associated with greater stream depth in the reaches farther upstream ($R^2 = 0.87$). Results at the reach scale suggested broad scale spatial segregation (1-10 km), particularly between larger and more phenotypically extreme individuals, whereas unit-scale results indicated spatial overlap between morphotypes within individual pools. These results provide the first perspective on spatial distributions and multi-scale habitat relationships of polymorphic mountain whitefish within a coastal riverscape.

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Introduction

Trophic polymorphism is a form of resource-based phenotypic diversification, with examples found in every class of vertebrate (Skúlason and Smith 1995, Smith and Skúlason 1996, Smith and Girman 2000). Trophic polymorphisms are most common among animals that subdue, handle and capture their prey with their mouth, such as birds, amphibians, and fishes (Wimberger 1994). Alternate phenotypes may be the result of differing selection pressures, adaptive morphological plasticity, genetic influence, or some combination of these factors (Robinson 1994, Smith and Girman 2000). Resource-based polymorphism typically occurs when exploitation of under-utilized resources ("open" niches) necessitates specific morphological characteristics. Morphological variation typically occurs in the head and mouth, and there are often associated differences in the body size in fishes (Wimberger 1994, Skúlason and Smith 1995, Smith and Skúlason 1996). The absence of competition for resources may facilitate the divergence of sympatric morphotypes (Jónsson and Skúlason 2000). Several authors have hypothesized that niche-based variation in feeding structures reduces intraspecific competition (Robinson 1994, McLaughlin et al. 1999, Swanson et al. 2003). If morphological traits important in resource use are correlated with traits that are important in mate and site selection, reproductive isolation may occur (Smith and Skúlason 1996), which may eventually lead to speciation (Skúlason et al. 1989, Robinson and Schluter 2000).

Fishes offer many examples of polymorphisms across taxa, particularly among species of cichlids in low latitudes (Kornfield et al. 1982, Liem and Kaufman 1984, Hori 1991, Klingenberg et al. 2003), and in recently glaciated lakes in high latitudes (Schluter and McPhail 1993, Robinson 1994). The post-glacial environment provides "open niches" for colonizing fish due to the absence of competition (Schluter and Rambaut 1996, Smith and Skúlason 1996). The spatially structured nature of the lacustrine environment (e.g., littoral, limnetic, and profundal habitats) provides a template for diversification, and has lead to alternate phenotypes of various species. Examples include, but are not limited to, lake whitefish (*Coregonus clupeaformis*), brook char (*Salvelinus fontinalis*), stickleback (*Gasterosteus aculeatus*), and Arctic char (*Salvelinus alpinus*) (Smith and Skúlason 1996). Resource polymorphisms in lakes are typically associated with spatially segregated littoral and pelagic habitats due to intraspecific variation in feeding structures. For example, the benthivorous form of Arctic char is associated with littoral habitat, whereas the planktivorous form is pelagic (Hindar and Jónsson 1993). The occurrence of sympatric morphotypes and absence of intraspecific competition may be maintained through spatial segregation of discrete foraging habitats (Smith and Skúlason 1996, Robinson and Schluter 2000, Davis and Pusey 2010). The degree of isolation (i.e., reproduction and feeding) may also vary among neighboring lakes (Bernatchez et al. 1999).

The physical habitat in riverine environments is often assumed to be less spatially structured than in lakes, and examples of trophic polymorphisms are few (but see Kondrashov and Mina 1986, McLaughlin and Grant 1994, Wimberger 1994, Davis and Pusey 2010). Despite the lack of barriers to dispersal found in lakes, habitat features in stream systems can be spatially heterogeneous (Poole 2002), and the diversity of habitat types may encourage resource polymorphisms (Smith and Skúlason 1996). Mountain whitefish (*Prosopium williamsoni*) provide an example of resource-based polymorphism in rivers, with one form that develops an elongated and slightly upturned snout (Evermann 1893, McPhail and Troffe 1998), coined the “pinocchio” form by Troffe (2000), which is distinguished from the normal form that does not develop an elongated snout and maintains an evenly sloped head shape. Mountain whitefish are widely distributed and abundant among temperate rivers in western North America (Northcote and Ennis 1994), and polymorphic mountain whitefish likely occur in drainages throughout their range (C. Baxter, Associate Professor of Ecology, Idaho State University Stream Ecology

Center; W. McMillan, Wild fish Conservancy, Seattle, WA; Shivonne Nesbit, Oregon Department of Fish and Wildlife, personal communication). Previous work has shown variation in feeding habits and diet among mountain whitefish that corresponded to a gradient of morphological variation (Troffe 2000, Whiteley 2007).

Morphological variation in mountain whitefish was originally thought to be the result of sexual dimorphism, with males developing the elongated snout (Evermann 1893), but recent studies have found that both sexes can have elongated snouts (Troffe 2000, McPhail and Troffe 2001). Observations on foraging tactics reported by Troffe (2000) from the upper Fraser River, British Columbia, indicated that the pinocchio form expended approximately half of its time foraging for benthic invertebrates by using the elongated snout to overturn substrate, whereas the normal form fed primarily on drifting invertebrates. Whiteley (2007) observed the greatest variation in snout morphology in the largest fish (> 47 cm), and the least amount of variation in the smallest fish (< 25 cm), and concluded that a stage-specific ontogenetic shift likely occurs between the ages 2 and 3. This range corresponds to shifts in diet (Pontius and Parker 1973), and patterns of habitat use (Northcote and Ennis 1994) from juvenile to adult life stages. As an individual moves from shallow to deeper water, divergent development of the snout occurs and leads to further specialization as the individual matures. However, the biotic interactions and environmental factors influencing variation in snout development have not been described.

Quantifying the spatial distribution of alternate morphotypes, and relationships with longitudinal variation in stream habitat characteristics is important for understanding the establishment and maintenance of polymorphic populations (Davis and Pusey 2010). Distribution and assemblage structure of fishes are generally thought to change gradually from headwaters to mouth (Horwitz 1978, Vannote et al. 1980, Hughes and Gammon 1987, Paller 1994, Belliard et al. 1997). The distribution of size classes is also thought to change along the longitudinal stream profile (Schlosser 1991), following a pattern of larger fish downstream (Welcomme 1985, Schlosser 1987b) and smaller fish upstream (Patrick 1975, Schlosser 1982, Power 1987). However, the opposite pattern (larger fish upstream) has been documented in New Zealand brown trout (*Salmo trutta*) (Jellyman and Graynoth 1994), and Arctic grayling (*Thymallus arcticus*) in Alaska (Tack 1974, Hughes and Reynolds 1994).

Our understanding of fish spatial distribution and relationships to their environment may be limited by traditional sampling techniques that employ random sampling of short reaches (< 500 m) that are widely spaced (> 10 km) (Fausch et al. 2002, Poole 2002). The distributions of stream fishes and aquatic habitats may be spatially heterogeneous (Townsend 1989, Schlosser 1991, Poole 2002). The response of biota to scale-dependent patchiness will vary according to the scale at which they perceive differences in their physical environment (Wiens 1989, Kotliar and Wiens 1990). Thus, the observed patterns of habitat associations and spatial distribution are governed by the scale of analysis, which in turn is constrained by the resolution (grain) and extent (spatial/temporal) of data (Fausch et al. 2002, Wiens 2002). Small-scale (or site-based) studies often indicate greater importance of biotic interactions (i.e., competition, predation), whereas large-scale studies typically place greater emphasis on environmental controls (Jackson et al. 2001). The traditional site-based approach provides a coarse-scale perspective of fish distribution, but does not account for fine-scale heterogeneity in fish abundance and patterns of habitat use (Fausch et al. 2002, Torgersen et al. 2006). A riverscape approach of spatially continuous sampling over a broad extent is one way to account for such heterogeneity (Torgersen et al. 1999), and may help answer questions about how the extent and resolution of sampling, as well as the scale of analysis, may influence our perceptions of distribution and habitat associations (Torgersen et al. 2006).

No studies have examined polymorphic fluvial whitefish within the context of habitat heterogeneity and size-class assemblage structure. In addition, information on coastal populations of mountain whitefish is lacking in the published literature. To elucidate relationships between physical habitat and spatial segregation between morphotypes it is important to assess these patterns at the appropriate spatial scale(s) (Fausch et al. 2002). In this study, I applied a modified version of a continuous riverscape sampling methodology to quantify habitat features and mountain whitefish abundance in the Calawah River, a coastal watershed on the Olympic Peninsula of Washington State, USA. The objectives of this study were to (1) evaluate differences in the spatial distribution of whitefish morphotypes and size classes, (2) describe the assemblage structure of morphotypes and size classes and their relationships with aquatic habitat, and (3) quantify the associations between the relative density of morphotypes and longitudinal variation in aquatic habitat. I hypothesized that (1) morphotypes would be associated with distinctly different habitat features based on previous studies of feeding behavior and diet, and (2) these differences in habitat association would segregate morphotypes at channel unit and reach scales. Specifically, I expected that normal whitefish would be associated with habitat related to feeding on drift, such as higher gradient reaches and larger substrate size, and that pinocchio whitefish would be associated with habitat related to benthic feeding, such as low gradient reaches with a greater percentage of pool habitat.

Methods

Study area

The South Fork (SF) Calawah and mainstem Calawah River flow westward for 33.8 and 18.3 km, respectively (Figure 1) from an elevation of approximately 1,143 m. They have a combined drainage area of 186.5 km^2 (De Cillis 1998, Hook 2004). The channel is very stable and moderately confined by relic terraces in the lower mainstem Calawah River, and generally confined by steep valley walls in the upper mainstem Calawah and SF Calawah Rivers. The hydrograph is strongly influenced by rainfall, with peak flows occurring in November and December (Hook 2004). The upper 25 km of the SF Calawah are located within the Olympic National Park (ONP)and the remainder, along with most of the Sitkum River, lies on federally owned forestland (U.S. Department of Agriculture Forest Service), and is managed as late successional forest reserve for spotted owls (De Cillis 1998, Hook 2004). Portions of the mainstem Calawah, SF Calawah, and Sitkum Rivers were burned in 1951 resulting in a loss of large woody debris recruitment and an increased potential for mass wasting events (De Cillis 1998). The area was then logged to remove dead and dying trees, and this further delayed recovery of riparian forests and recruitment of instream large woody debris (De Cillis 1998, Hook 2004). The mainstem Calawah River flows through privately managed forests that are actively harvested on a 35-40 year rotation (Hook 2004). The riparian forest is dominated by Sitka spruce (*Picea sitchensis*), red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), western red cedar (*Thuja plicata*), and Douglas fir (*Pseudotsuga mensiesii*) in the lowlands with western hemlock (*Tsuga heterophylla*) and silver fir (*Abies amabilis*) in the higher elevations (Smith 2000).

In addition to mountain whitefish, the Calawah River and its tributaries support populations of summer and winter steelhead (*Oncorhynchus mykiss*), coastal cutthroat trout (*O. clarkii clarkii*), fall coho salmon (*O. kisutch*), and fall and summer chinook salmon (*O. tshawytscha*) (Hook 2004). A small population of river-type sockeye salmon (*O. nerka*) spawns annually in the SF Calawah. Non-salmonids include Pacific lamprey (*Lampetra tridentata*), western brook lamprey (*L. planeri*), speckled dace (*Rhinichthys osculus*), longnose dace (*R. cataractae*), and several species of sculpin (Cottidae).

Visual surveys of fish and aquatic habitat

Spatially continuous snorkel and habitat surveys were conducted on August 16-19, 2010 during summer base flow (1.84 m^3/sec^{-1}, USGS gauging station 12043000) over approximately 29 km of the mainstem and SF Calawah river. I used snorkeling methods developed in previous studies (Thurow 1994). Snorkeling offers an alternative to electrofishing and provides a relatively accurate and highly efficient method for enumerating salmonids in streams that are either too small to sample with a boat-mounted electrofisher, or too large to sample with a backpack electrofisher (Cunjack et al. 1988, Zubick and Fraley 1988, Thurow and Schill 1996, Mullner et al. 1998, Joyce and Hubert 2003). To reduce potential observational bias between multiple divers, a single experienced diver sampled all sites (Hankin and Reeves 1988). Sampling began within the boundaries of the ONP, 4 km upstream from the confluence of the SF Calawah and Sitkum Rivers (47° 56′ N, 124° 12′ W), and ended approximately 2 km upstream from the confluence of the mainstem Calawah River and Bogichiel River (47° 56′ N, 124° 26′ W, Figure 1). The total extent of the survey was approximately 29 km, and 225 channel units were sampled; 8 units were < 0.25 m deep and could not be sampled. The final 2 km of the lower mainstem Calawah River were not sampled because the channel was too deep (> 5 m) and wide (> 40 m) for a single diver (Thurow 1994).

Snorkel surveys began at 9:00 and were completed each day by 16:00 to avoid diurnal and crepuscular movement patterns of salmonids (Wootton 1998). Counts of whitefish morphotypes were recorded in each channel unit (i.e., pool and non-pool), and fish that were intermediate between pinocchio and normal in terms of snout length were included with the pinocchio count (Figure 2). In addition to head shape, pinocchio whitefish were distinguished from normal whitefish by the presence of highly visible white scar tissue on the tip of the snout.

To avoid bias associated with estimating fish size underwater (Edgar et al. 2004), three size classes were used that were easily distinguishable underwater (Table 1). All surveys were conducted by the diver moving downstream, typically within a single pass adjacent to the thalweg. In locations with high salmonid density and/or presence of instream cover, the diver made a second pass and averaged the two counts (Thurow 1994).

In each sampled channel unit, a bank technician collected data on unit length, wetted width, maximum depth, and channel slope, and the diver provided a visual estimate of substrate composition and instream cover. Maximum unit depth was measured with a stadia rod, and gradient was measured with a stadia rod and clinometer. Length and width were measured with a laser rangefinder. Substrate composition was visually estimated as a percent of pebble, cobble, boulder, and bedrock. The dominant substrate of each channel unit was assigned a rank based on median size: pebble (16-64 mm) = 1, cobble (64 – 256 mm) = 2, boulder (> 256 mm) = 3, and ties were averaged (Allan 1995).Bedrock substrate was converted to a binary variable (i.e., present or absent) because it did not constitute a significant portion of the streambed surface area (i.e., <10%), and typically was covered by a lens of cobble or pebble. Breaks between each channel unit were mapped with a global positioning system (GPS; Garmin III). Field measured length was corrected with map distances using GPS point data in ArcView GIS (version 9.1, ESRI 2004) and high resolution digital ortho imagery (USDA 2009). Channel units were classified as either a pool or non-pool. A pool was defined as a habitat unit with smooth surface flow, a maximum depth that was at least 25% of bankfull depth, and length or width that was at least 10% of bankfull width (Montgomery et al. 1995). Channel type was identified as pool-riffle, forced pool-riffle, or plane bed (Montgomery and Buffington 1997).

Data standardizations and transformations

Data collected at the unit-scale were binned into approximately 1-km reaches for analysis of distribution, assemblage structure, and habitat associations. The length of each bin was determined according to changes in channel morphology, including major tributary junctions, and natural breaks in channel and unit type. Channel type was calculated as a percentage of total bin length, and pool area was calculated as a percentage of total bin area. Floodprone and bankfull width were measured on high resolution digital ortho imagery (USDA 2009). Bankfull width, floodprone width, valley width index, substrate score and maximum unit depth were averaged for each bin. Bin gradient was derived by multiplying unit-scale gradient by length, summing across all units within the bin, and dividing by total bin length. Counts of mountain whitefish were summed for each bin and standardized in two different ways. First, data were column standardized (percent cumulative abundance), and plotted versus distance upstream for comparison of spatial distributions in SigmaPlot, version 10.0 (SYSTAT 2006). Second, abundance data were standardized as relative density (D_r) at both the unit and reach scales to account for variation in unit and bin length, and to reduce variance in the datasets (Brenkman et al. 2012). At the unit scale, morphotype relative density was calculated for quantifying differences between habitat types:

$$(1)\ D_r = \left(\frac{f_i}{l_i}\right) / \left(\frac{f_t}{l_t}\right)$$

where f_i = number fish per channel unit, l_i =length (m) of channel unit, f_t = total number of fish, and l_t = total length (m) sampled. At the reach scale, relative density was calculated in a similar fashion where f_i = number fish per 1-km custom bin, l_i =length (km) of custom bin, f_t = total number of fish, and l_t = total length (km) sampled. Positive and negative values of relative density indicated densities of mountain whitefish that were above and below the average density for the entire length of stream sampled, respectively (Brenkman et al. 2012). Relative density was highly skewed (leptokurtic) at both the unit and reach scales, and therefore was transformed using the natural logarithm (x_i + 1) for subsequent analysis (Zar 1984). To reduce variance and normalize distribution, mean reach-scale channel and floodprone widths were transformed using the natural logarithm (Zar 1984).

Statistical analysis

Assemblage structures of normal and pinocchio whitefish size classes were assessed with non-metric multidimensional scaling (NMS) in the statistical software R (R Core Development Team 2009), using the “vegan” package (Oksanen et al. 2010). NMS is a useful tool in community ecology for analysis of data that violates the assumption of multivariate normality (McCune and Grace 2002, Kenkel 2006). NMS uses the rank order of distances to represent objects in multivariate space (Kruskal and Wish 1978, Digby and Kempton 1987), rather than the actual distance (e.g., Euclidean) used in other multivariate variance partitioning methods (e.g., principal components analysis). I used the Bray-Curtis distance coefficient, a distance measure commonly applied to count data with zero values, and 10,000 iterations to avoid reaching a local minimum in stress (Legendre and Legendre 1998). Complete absence of all “species” (i.e., row sum of observations = 0) cannot be calculated as a distance coefficient in multivariate analysis. Therefore, bins (n = 5) were removed from the reach-scale multivariate data set, which corresponded to the upper SF Calawah River (distance upstream > 25 km) and the lower SF Calawah River. A two dimensional ordination was used in the analysis to simplify interpretation. Although additional dimensionality did result in a lower stress value, this did not change the dominant gradients of variation. Centroids of size classes and morphotypes in ordination space were plotted in conjunction with vectors representing correlations between axis scores and a second matrix of environmental variables (i.e., variable loadings).

Unit-scale differences in the relative density of normal and pinocchio whitefish (all size classes combined) between pool (n = 46) and non-pool (n = 124) habitats were quantified with a Wilcoxon rank sum test in the statistical software R using the base “stats” package (R Core Development Team 2009). Channel units in the mainstem Calawah and lower SF Calawah that were too shallow to snorkel (< 0.25 m, n = 3), and units within the upper SF Calawah where whitefish were absent (n = 59), were removed from the dataset prior to analysis. Box and whisker plots were used for graphical representation of differences in relative density between each morphotype.

Modeling of fish–habitat associations

I quantified reach-scale associations between the relative density of morphotypes with respect to environmental variables using a series of generalized additive models (GAMs) in R (R Core Development Team 2009), with the “mgcv” package (Wood 2006). The default smoothing function, thin-plate penalized regression splines (Wood 2003), was used to model non-linear relationships with a Gaussian error distribution and identity link function:

$$(2)\ \ \delta(\mu_i) = \beta_0 + s1(x1_i) + s2(x2_i) + \cdots$$

where $E(y_i) \equiv \mu_i$, y_i are the independent observations, δ is a “link-function” (identity in this case), β_0 is the intercept, and s_1 is a smoothing function for the linear predictor x_1 (Wood 2001).

GAMs have several advantages over the commonly used generalized linear model (GLM) when testing for species habitat relationships, particularly when data are collected continuously over a large extent (Hastie and Tibshirani 1990). The response of an organism to its environment in nature may not be a simple linear or curve-linear relationship. A GAM provides a less restrictive non-linear approach to modeling in which the data determine the shape of the relationship (versus the limited response shapes in a parametric model) through a series of smoothing splines (Hastie and Tibshirani 1986, 1990). Smoothed estimates are based on a weighted average of neighboring observations using a back-fitting algorithm (Hastie and Tibshirani 1987). This approach is particularly useful when the form of the relationship between the response and predictor variable is unknown (Yee and Mitchell 1991, Knapp and Preisler 1999). The form of the relationship may range from a straight line to increasingly complex non-parametric curves.

Spatial autocorrelation, in which relationships between samples are a function of the distance separating them, is common in data collected in a spatially continuous manner; this potentially violates the assumption of independence in statistical analyses (Legendre 1993). One approach to correct for spatial autocorrelation is to explicitly incorporate spatial structure in the statistical model (Legendre 1993). I used GAMs to demonstrate that distance upstream was significantly associated with both normal and pinocchio whitefish relative density ($p < 0.01$). I then extracted the model residuals to evaluate spatial autocorrelation using variograms (Palmer 2002) with the “variog” function in the “geoR” package (Ribeiro and Diggle 2001) in R (R Core Development Team 2009). I assessed semi-variance at multiple lag intervals and distances, and determined that the residuals did not display strong spatial dependence. Therefore, I included distance upstream as a covariate to control for spatial autocorrelation when quantifying associations between whitefish abundance and physical habitat characteristics.

I visually examined spatial patterns of physical habitat features in relation to patterns in the relative density of whitefish. Physical habitat was modeled as a response to distance upstream using the thin-plate penalized regression spline smoother in the “mgcv” package (Wood 2006) in R (R Core Development Team 2009). Resulting spatial patterns of physical habitat provided contextual understanding of the modeled relationship between the relative density of whitefish and distance upstream. Substrate score was modeled as a function of distance upstream (Figure 6a) and displayed a spatial pattern of peaks and troughs (i.e., larger and smaller substrate size). However, the relationship in the GAM was only significant when the effect degrees of freedom (i.e., 'knots') was > 9, and the linear correlation was not significant ($r^2 = 0.003$, $p > 0.1$). Mean maximum depth (Figure 6b) did not display a strong spatial pattern ($r^2 = 0.05$, $p > 0.1$) in the GAM. Therefore, I assumed that including either substrate or depth in an additive model with distance upstream would not result in inflated variance due to co-linearity.

Prior to fitting models for each morphotype, Pearson correlations among independent variables were examined (Table 3), and highly correlated variables ($r > 0.3$) were excluded. I first analyzed associations with each physical habitat variable individually, including distance upstream as the first covariate in each model to de-trend spatial patterns. The variables that explained the most variance in each normal and pinocchio whitefish GAM were used in a model of the alternate morphotype to determine how relationships with the same variables differed between morphotypes. I then used stepwise forward-variable selection and analysis of deviance (ANODEV) with an approximate χ^2 test, (Hastie 1991) to select a suite of physical habitat variables that were associated with each morphotype. Fitted values and standard errors from the best GAMs for normal and pinocchio whitefish were back-transformed and plotted versus distance upstream (x-axis) in SigmaPlot (SYSTAT 2006) using locally weighted scatterplot smoothing (LOWESS) (Trexler and Travis 1993) with a second-degree polynomial smoothing parameter. Observed values were included in plots to evaluate how well each GAM predicted the locations and magnitudes of peaks and troughs in the relative density of normal and pinocchio whitefish.

Results

Mountain whitefish abundance was dominated by pinocchio whitefish (75% of all individuals), and nearly 50% of all whitefish counted were medium-sized pinocchio whitefish (Table 1). Neither form was seen in the SF Calawah River upstream of the confluence with the Sitkum River. Spatial distributions and relationships with physical habitat differed between pinocchio and normal whitefish. Normal whitefish were distributed farther downstream than pinocchio whitefish, and large size classes of both morphotypes were distributed farther downstream than small and medium size classes (Figure 3). In GAMs, normal whitefish were associated with substrate size and bedrock occurrence (Figure 7b), whereas pinocchio whitefish were associated with mean maximum depth (Figure 8d). The best model predicting the relative density of pinocchio whitefish based on aquatic habitat explained more variance than the best model for normal whitefish (Table 4).

Longitudinal distribution of whitefish size classes

Spatial patterns of small and medium size classes of normal whitefish were similar; 50% of small and medium normal whitefish were in the lower 9.6 km and 10.7 km of the study area, respectively (Figure 3). Small and medium size classes reached 75% of their cumulative abundance at 13.5 km upstream. The distribution of the large normal whitefish differed from small and medium size classes, such that the small and medium size classes were distributed much farther upstream (24.1 km, and 25.1 km, respectively) than the large size class. Fifty percent of normal whitefish in the large size class were in the lower 6.6 km of the study area, and their distribution extended 16.4 km upstream, approximately 1 km upstream of the confluence with the SF Calawah (15.6 km). There were also several marked increases in the longitudinal pattern of cumulative abundance for large normal whitefish, including an increase from 50% to 80% cumulative abundance at 7.8 km.

Pinocchio whitefish displayed size class distribution patterns similar to those of normal whitefish (i.e., small and medium sized fish upstream, and larger fish downstream). However, small and medium size classes of pinocchio whitefish were distributed farther upstream than those of the normal whitefish. Approximately 50% of the small and medium pinocchio whitefish were distributed in the lower 13.1 km and 12.8 km, respectively. Small pinocchio whitefish reached 78% in cumulative abundance at 14.9 km, and medium pinocchio whitefish reached 76% in cumulative abundance at 15.2 km. Pinocchio whitefish in both small and medium size classes extended 25 km upstream to the confluence with the SF Calawah River and Sitkum River. The distribution of the large pinocchio whitefish was similar to the distribution of medium-sized normal whitefish. Large pinocchio whitefish reached 51%, 75% and 100% in cumulative abundance at 9.0 km, 14.1 km, and 25 km upstream, respectively.

Size class assemblage structure

Multivariate ordination with NMS provided evidence of spatial segregation among morphotype size classes (Figure 4). Centroids of normal whitefish size classes were grouped in the upper left quadrant of the ordination plot. Small and medium size classes of normal whitefish were associated with both reach gradient and mean maximum depth, whereas the large size class was associated with reach gradient. All three size classes of normal whitefish were inversely associated with distance upstream, and were similar to patterns of cumulative abundance for large whitefish, which were highly inversely correlated with distance upstream. Pinocchio whitefish size classes were grouped in the lower two quadrants of the ordination plot. Small and medium size classes of pinocchio whitefish were associated with mean maximum depth and percent pool area. Large pinocchio whitefish were associated with distance upstream and percent pool area. All three size classes of pinocchio whitefish were more closely associated with distance upstream than normal whitefish. The grouping of size classes by morphotype indicated that combining size classes was appropriate for analyses of habitat associations at unit and reach spatial scales.

Habitat associations

Wilcoxon rank sum tests revealed no significant difference ($p < 0.05$) in relative density of normal whitefish between pool and non-pool habitats (Figure 5a; $p = 0.34$, W = 3085). However, there was a significant difference in the relative density of pinocchio whitefish between habitat types (Figure 5b; $p < 0.0001$, W = 1084), which tended to be greater in pool habitat than in non-pool habitat. Additionally, there was no overlap in the 25th and 75th percentiles of pinocchio whitefish relative density between non-pool and pool habitat types, providing further evidence of pinocchio whitefish using pool habitat more than non-pool habitat.

In generalized additive modeling, variation in the relative density of normal whitefish was best explained by distance upstream, substrate size (an increase in substrate score is synonymous with an increase in size), and a linear coefficient for the occurrence of bedrock substrate (Figures 7a and 7b; $R^2 = 0.64$). The association between normal whitefish relative density and substrate, given the effects of distance upstream and bedrock occurrence, was positive up to a substrate score of 2.4 (analogous to reaches dominated by boulder and boulder/cobble mix); at substrate scores greater than 2.4 there was an inverse relationship between substrate size and normal whitefish relative density. Distance upstream, substrate size, and bedrock occurrence resulted in 46%, 14%, and 18% reductions in deviance, respectively

(Table 4). No other variables were significantly associated with the relative density of normal whitefish.

The relative density of pinocchio whitefish was positively associated with distance upstream (after accounting for the effect of substrate size) to approximately 13 km, and was negatively associated with distance upstream to 29 km (Figure 7c). However, there was no significant association with substrate size (Figure 7d; $R^2 = 0.59$). Pinocchio whitefish relative density variation was best explained by distance upstream and mean maximum depth (Figures 8c and 8d; $R^2 = 0.87$). Pinocchio whitefish displayed a strong positive curve-linear relationship with mean maximum depth, with higher densities in reaches with a mean maximum depth ≥ 1.2 m. In contrast, there was a weak positive linear relationship ($R^2 = 0.47$) between normal whitefish relative density and mean maximum depth (Figure 8b), after accounting for the effect of distance upstream (Figure 8a). Mean maximum depth and distance upstream in the GAM for pinocchio whitefish resulted in 67% and 24% reductions in deviance, respectively (Table 4). Outliers were omitted from Figure 7c (x = 13, y = 8.8, and x = 15, y = 12.7), Figure 7d (x = 3.2, y = 4.9), Figure 8c (x = 15, y = 5.8), and Figure 8d (x = 2, y = 7.7). No other variables were significantly associated with pinocchio whitefish relative density.

Plots of fitted and observed whitefish relative densities versus distance upstream indicated that the GAM for normal whitefish accurately predicted the locations of peaks and troughs in whitefish relative density (Figure 9). However, this model was not able to predict the magnitudes of peaks and troughs in relative density. For example, the three highest peaks in observed normal whitefish relative density exceeded the standard error interval. In contrast, the pinocchio whitefish GAM accurately predicted both the locations and the magnitudes of peaks and troughs in relative density. Nearly all of the observed values for pinocchio whitefish relative density were within the standard error intervals, and the second highest observed peak in pinocchio whitefish relative density corresponded exactly to the fitted value.

Discussion

Spatial segregation

Results from this study indicated that pinocchio and normal mountain whitefish morphotypes had different spatial distributions that were associated with differences in habitat relationships at channel unit and reach scales. Distribution patterns at the reach scale suggested that there was spatial segregation of whitefish morphotypes at a broad scale (1-10 km). Normal whitefish were more abundant in the lower Calawah River, and pinocchio morphotype fish were more abundant in the upper Calawah River and the lower SF Calawah River. No whitefish were found in the upper SF Calawah where mean wetted width was < 10 m. Although there are no previous studies on the spatial distribution of polymorphic whitefish in rivers, the results corroborate other reports that mountain whitefish are generally found lower in the watershed and in mainstem habitats (Platts 1979, Maret et al. 1997, Meyer et al. 2009). Smaller tributaries may not provide suitable habitat conditions, such as adequate depth and cover for mountain whitefish (Sigler 1951). However, McPhail and Troffe (1998) found that mountain whitefish occupied smaller streams (5-10 m wetted width) in British Columbia (Canada), and Idaho (USA) (Meyer et al. 2009). The species also has been observed in small tributaries (mean wetted width < 10 m) within the Calawah and Hoh River drainages during late winter and spring (J. Starr, personal observation). Meyer et al. (Meyer et al. 2009) speculated that whitefish in the southern portion of their range typically occupy larger streams, whereas whitefish in the northern portion of their range generally occupy smaller streams. However, coastal mountain whitefish may move into smaller streams after they spawn in the fall to seek refuge during periods of higher flow in winter and spring.

There was a longitudinal pattern of larger fish downstream and smaller fish upstream in both forms. For example, large pinocchio whitefish overlapped with small- and medium-sized normal whitefish. Similar patterns with large individuals downstream have been documented for other species (Patrick 1975, Schlosser 1982, Power 1984, Welcomme 1985, Schlosser 1987a). In contrast to these studies, a pattern of larger fish upstream was observed in New Zealand brown trout (*Salmo trutta*) (Jellyman and Graynoth 1994), and in Alaska with Arctic grayling (*Thymallus arcticus*) (Tack 1974, Hughes and Reynolds 1994). Results from this study suggest that large bodied mountain whitefish (regardless of morphotype) may require a greater volume of habitat during summer base flow conditions, perhaps to balance the trade-offs between predation risk and foraging opportunities. In addition, the aforementioned studies which documented a larger-fish-upstream pattern were based on the traditional sampling approach of widely spaced reaches, and may not have captured the heterogeneous nature of fish distribution (Poole 2002).

Small and medium size classes of both morphotypes had similar spatial distributions compared to the large size classes of normal and pinocchio whitefish, which were distributed farther downstream. The differences between small and large size classes that I observed were similar to the observations by Whiteley (2007), who found that morphological and dietary variation was the greatest in larger individuals (> 47 cm), and the least in smaller individuals (< 25 cm). Although the observed spatial pattern of cumulative abundance among size classes corresponded with this spectrum of size-related morphological variation, the total abundances did not. If variation is least pronounced in smaller individuals, we may expect that the abundance of smaller normal whitefish would be greater in this size class. However, the total abundance of small (10 – 29 cm) pinocchio whitefish was twice that of small normal whitefish. It is possible that juvenile mountain whitefish in low-elevation coastal river systems, specifically on the Olympic Peninsula, undergo more rapid growth as young of the year and juveniles and make this shift in feeding habits earlier in their ontogeny (McHugh 1942). Currently, there is limited information on growth and maturation of coastal mountain whitefish populations, and more research in this area is needed.

Pinocchio and normal whitefish were generally spatially segregated at broader scales, but not necessarily at smaller scales. For example, pinocchio whitefish relative density was significantly greater in pool habitat than in non-pool habitat, but normal whitefish relative density was not significantly different between pool and non-pool habitats. Thus, at smaller scales, the two morphotypes overlapped in individual pools. Given the reach-scale distribution pattern, it is likely that this overlap occurs in the lower mainstem Calawah where normal whitefish were more abundant. Differences in patterns of distribution and habitat use may be a function of the scale (Feist et al. 2003, Berger and Gresswell 2009). For example, Feist et al. (2003) found that reach-scale models of spring/summer chinook redd densities provided less predictive power compared to watershed-scale models. Results from my study highlight the need to collect spatially continuous data over a broad extent, and at the finest grain size possible to allow data to be examined at multiple spatial scales.

Assemblage structure and relationships to aquatic habitat

Results from my study indicated the presence of distinct size class assemblages of whitefish morphotypes. There was a consistent correspondence between small and medium size classes, compared to the large size class, which differed significantly from the smaller size classes in ordination space. The positive association between depth and the small and medium size classes of both morphotypes provided further evidence of unit-scale spatial overlap between whitefish morphotypes in deep-water habitat (i.e., pools). These results suggest that habitat use becomes more specialized in larger individuals that are more phenotypically extreme, i.e., have more pronounced, elongated snouts. These results support the findings by Whiteley (2007), in which larger individuals (> 47 cm) displayed greater morphological variation that was associated with significant differences in diet. Whiteley (2007) concluded that a stage-specific ontogenetic shift that occurs at approximately three years of age (i.e., 22-24 cm in length) may lead to phenotypic diversification. There may be a significant dietary shift between juvenile and adult life stages (Pontius and Parker 1973) that corresponds with a change in habitat use from shallow, marginal habitat to deeper and faster habitat in the main channel (Northcote and Ennis 1994). Although the positive association between gradient and large normal whitefish may be a departure from the typical relationship between whitefish and depth, this association does suggest that normal whitefish may be using high-gradient reaches for their high rates of invertebrate prey delivery (Troffe 2000).

Reach-scale habitat associations

When all size classes were combined in a model of relative density, normal whitefish were associated with larger substrate (Figure 7b), which was positively correlated with gradient (Table 3). The normal whitefish GAM also fitted a peak in relative density located in the lower Calawah River, providing further evidence of a downstream pattern in distribution. In my study, it is possible that deeper, fast-water habitat, combined with large boulder substrate in the lower Calawah River provided better foraging opportunities for drifting invertebrates preferred by normal whitefish (sensu Troffe 2000, Whiteley 2007). However, distance upstream, substrate, and bedrock occurrence explained only 64% of the variation in relative density, suggesting that other variables (e.g., temperature, primary production, and aquatic invertebrate communities) not considered in this study may explain additional longitudinal variation in the abundance of normal whitefish. The weak linear relationship between normal whitefish relative density and depth was inconsistent with observations by Troffe (2000), who observed normal whitefish feeding primarily on drift (Troffe 2000). However, the relationship that I observed may be due to the greater abundance of medium and small size classes of normal whitefish (Table 1), which displayed a stronger correlation with depth than the large size class (Figure 4). The inverse relationship between normal whitefish and substrate beyond the score of 2.4 was not expected; however, interpretation of this result is difficult due to the lack of data points.

Pinocchio whitefish relative density increased strongly with mean maximum depth. Mountain whitefish have been shown to be associated with greater depth (DosSantos 1985, Wydoski and Whitney 2003, Torgersen et al. 2006), and it has been speculated in other studies that deep pools provide adequate cover for the species (Sigler 1951). The pinocchio whitefish GAM fitted a peak in the relative density located in the upper Calawah and SF Calawah Rivers. Bedrock outcroppings and forced pool-riffle channel morphology dominate these river segments, creating deep scour pools that provide slower velocities, cover from predators, and small-diameter substrate. Deep pools with small diameter substrate in low gradient reaches may provide the habitat conditions that pinocchio whitefish require to overturn substrate and forage for benthic invertebrates (Troffe 2000). I observed individual pinocchio whitefish using their snout to overturn pebbles and small cobbles, but I did not quantify the extent of this behavior. In my study, depth and distance upstream explained 87% of the variation in the relative density of pinocchio whitefish at the reach scale, and relative density was significantly higher in pool habitat at the unit scale. These results suggest that pinocchio whitefish may have narrow habitat requirements during periods of low flow in summer months. Deep pools also may offer thermal refuge for salmonids during peak summer temperatures (Berman and Quinn 1991, Nielsen et al.

1994, Ebersole et al. 2003). Thermal habitat segregation has been documented in lake dwelling morphotypes of Arctic char, with smaller ‘pale’ individuals occupying cooler habitats in the hypolimnion and larger ‘dark’ individuals occupying warmer habitats found in the epilimnion (Power et al. 2012). In July 2010 in the SF Calawah River, I observed a large school of pinocchio whitefish holding on the bottom of a thermally stratified pool that was 20.6° C on the surface, and 13.5° C on the bottom at a depth of nearly 5 m.

Previous studies have reported on various feeding habits and relationships between mountain whitefish and instream characteristics (Northcote and Ennis 1994). The species is often associated with greater stream width, lower gradient, deep pool habitat (Sigler 1951, Platts 1979, Wydoski and Whitney 2003, Meyer et al. 2009), and small substrate size (DosSantos 1985). However, mountain whitefish have also been associated with higher-gradient shallow habitats (e.g., runs and riffles) (Stuart and Chislett 1979, Torgersen et al. 2006). Thompson and Davies (1976) found that Sheep River mountain whitefish occupied positions in the water column that were 2 to 10 cm from the stream bed while they were feeding on drifting invertebrates; none of these whitefish were observed feeding on benthic invertebrates, although gravel or sand occurred in the stomach contents of 54% of the fish examined. In contrast, Dos Santos (1985) found that mountain whitefish in the Kootenai River fed disproportionately on chironomids, and underwater observations revealed that these fish were using their snout to overturn smaller substrate. Differences in habitat relationships and feeding behavior described in the aforementioned studies may be explained in part by specific polymorphic associations with habitat unique to a given basin or sub-basin.

In my study, spatially continuous sampling provided insight regarding the overall population structure of polymorphic whitefish, which was dominated by the pinocchio form (Table 1). It is likely that the unique characteristics a given river supports differing degrees of morphological variation, e.g., the pattern of variation observed among lake whitefish in northern postglacial lakes (Bernatchez et al. 1999). The Calawah River and SF Calawah River have substrates that form a lens of cobble and pebble over bedrock, and are dominated by low-gradient pool-riffle and forced pool-riffle channel morphologies that favors the pinocchio foraging tactics. These channels are intersected by shorter, higher gradient plane bed reaches that contain large boulders, and thus provide a geomorphological template that favors the feeding behavior of normal whitefish.

In this study, I did not examine the full spatial and temporal distribution of mountain whitefish within the Calawah watershed. The grain and extent of sampling has been shown to affect observed species-habitat relationships (Wiens 1989, Kotliar and Wiens 1990). Mountain whitefish occupy portions of the lower North Fork Calawah River, the Sitkum River, and have been observed farther upstream of the survey extent in the SF Calawah (J. Starr, personal observation). Because mountain whitefish occur in neighboring drainages within the Quileute basin, my study also did not account for basin-scale factors affecting the spatial distribution of whitefish. I also did not account for temporal variation in fish distribution (e.g., seasonal migration), which is an important factor that may influence salmonid distribution (Schlosser 1985, Taylor et al. 1996, Dunham et al. 2002, Dunham et al. 2007) (see Appendix A for spring-summer variation in distribution).

In my snorkeling surveys of whitefish distribution and abundance, I did not account for sampling efficiency by using alternative methods to verify whitefish counts and sizes. Habitat size and complexity, fish species and size, density, and the intensity of sampling effort may affect the efficiency of snorkeling estimates of fish abundance (Riley and Fausch 1992, Rodgers et al. 1992, Bayley and Dowling 1993, Peterson et al. 2004). . Studies have shown that snorkeling efficiency is greatest in small streams (Orell and Erkinaro 2007), and where underwater visibility is high enough for the diver to view both stream banks (Zubick and Fraley 1988). Efficiency is reduced in deeper, wider mainstem river sections, and particularly in turbulent fast-water (Orell and Erkinaro 2007) where multiple divers may be required to effectively sample all possible portions of the stream channel (Hagen and Baxter 2005). In my study, one highly experienced diver conducted all of the snorkel surveys; therefore my sampling bias is expected to be consistent. However, due to the difficulties of sampling wide and deep sections of the river with only one diver, my estimates of fish abundance in the lower mainstem Calawah River are likely to be negatively biased.

Implications for management and conservation

Across their range, mountain whitefish play an important role in stream ecosystems, but their ecology is still not fully understood. As more is learned about the species, mountain whitefish may be increasingly considered by conservationists and fisheries managers. Fluvial mountain whitefish spend their entire lives in the freshwater environment and have been reported to live up to 29 years (McHugh 1942, McAfee 1966, Nelson and Paetz 1992). Consequently, mountain whitefish have been identified as a potential indicator species of riverine habitat conditions and water quality (McPhail and Troffe 1998, Cash et al. 2000, Meyer et al. 2009). Studies indicate that mountain whitefish exhibit homing behavior associated with summer rearing and fall spawning locations, and that they are capable of extensive annual migrations within a stream network (Petit and Wallace 1975, Davies and Thompson 1976, McPhail and Troffe 1998, Baxter 2002). Migratory mountain whitefish may represent significant vectors of nutrient transport within a watershed (Baxter 2002, Lance and Baxter 2011). Movement by mountain whitefish throughout stream networks during different life stages suggests that they may require a watershed-scale approach to conservation that has been applied to Pacific salmon (Roni et al. 2002).

Mountain whitefish have been studied extensively in interior rivers (e.g., east of the Cascade Mountains and in the Rocky Mountains), yet comparatively little is known about their ecology in coastal watersheds of the USA. The Olympic Peninsula in western Washington offers a unique example of coastal mountain whitefish populations (Northcote and Ennis 1994). Whiteley et al. (2006) found that whitefish from the Hoh River basin which flows into the Pacific ocean on the western side of the Olympic Peninsula were genetically related to the coastal population of mountain whitefish in the lower Fraser River in British Columbia, Canada. However, whitefish from the North Fork Skokomish River that flows into the Hood Canal on the eastern side of the Olympic Peninsula were more closely related to populations west of the Cascade Mountains in Oregon, Washington, and British Columbia. Beyond range-wide genetic assessments, there have been no other studies of mountain whitefish in the coastal regions of Washington, Oregon, and northern California.

Mountain whitefish often constitute the majority of salmonid biomass in river systems in the Pacific Northwest. Lance and Baxter (2011) found that the species constituted over 50% of the salmonid biomass within an Idaho watershed, with a N:P ratio significantly greater than other bony fishes and similar to sympatric salmonids. This suggests that mountain whitefish represent an important assemblage of nutrients and energy in stream ecosystems. Mountain whitefish in medium to large coastal rivers (15-40 m wetted width) may compose an even greater proportion of salmonid biomass. In my study, mountain whitefish accounted for 66% of the total salmonid abundance, and whitefish abundance was dominated by the medium size class (61%; see Appendix A, Table A1). In contrast, total trout abundance was dominated by the small size class of rainbow trout (81%). I did not collect samples of live fish to record length and weight data;

however, my results suggest that biomass was dominated by whitefish, and it is likely that mountain whitefish are playing an important role in coastal river ecosystems.

Conclusions

The results from my study provide an important perspective on coastal mountain whitefish ecology, including the spatial distributions of alternative morphotypes, size class assemblages, and associations with aquatic habitat at multiple spatial scales. Broad-scale spatial segregation of phenotypically extreme individuals (i.e., those with more pronounced, elongated snouts), and the differing habitat associations of the two morphotypes may have the ecological function of reducing intraspecific competition and maintaining phenotypic diversity. Differing habitat associations also suggested that whitefish may be highly effective at obtaining food in habitats in which their morphology yields a functional advantage over other salmonids, and this may help explain why mountain whitefish are often more abundant than sympatric salmonids in rivers across their range. However, results at the unit-scale suggest that the two forms overlap within individual pools, suggesting that morphological expression, and thus feeding behavior, may be highly plastic. The degree of reproductive isolation (spatial or temporal) between the two morphotypes is also unclear, therefore genetic controls on phenotypic diversification remain unknown. Because mountain whitefish are broadcast spawners, reproductive isolation between morphotypes may be very limited (Whiteley 2007). Additional investigation on reproductive behavior is needed to determine the degree of spatial and temporal isolation between morphotypes. Condition factor (i.e., lipid levels), growth, movement, and survival of the two morphotypes at juvenile and adult life-stages also require further examination to elucidate the physiological tradeoffs of phenotypic diversification. Spatially explicit data on basin-wide abundance collected in conjunction with detailed information on movement, growth and survival may be required to identify the mechanisms that maintain the phenotypic plasticity found in mountain whitefish. Coastal mountain whitefish constitute an important component of the biomass and ecological complexity of river systems in the Pacific Northwest. Future efforts to conserve and protect coastal watersheds from increasing anthropogenic influences will need to consider mountain whitefish along with salmon and trout.

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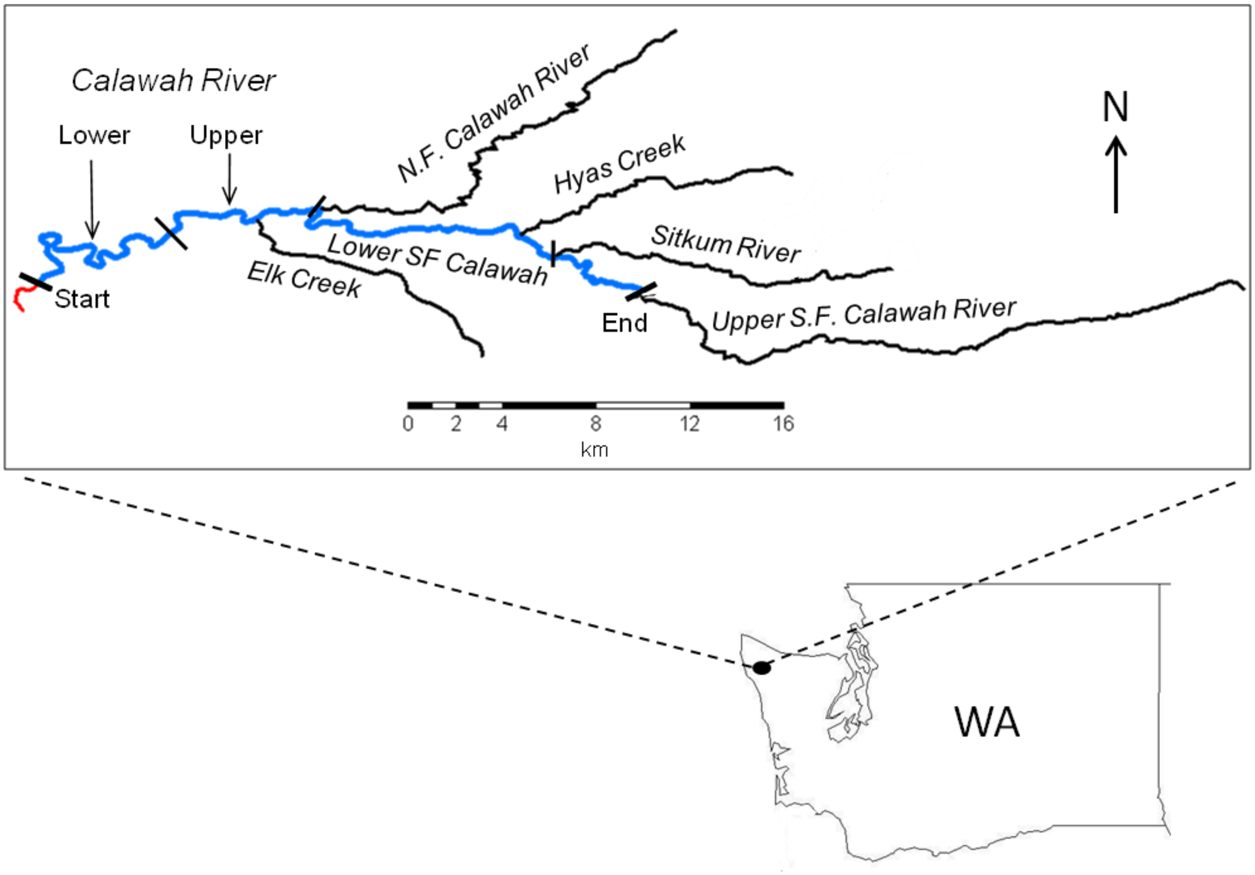

Figure 1. Location of the Calawah River on the Olympic Peninsula in Washington State, USA. The blue line represents the sampled stream length in the mainstem Calawah River and South Fork Calawah River.

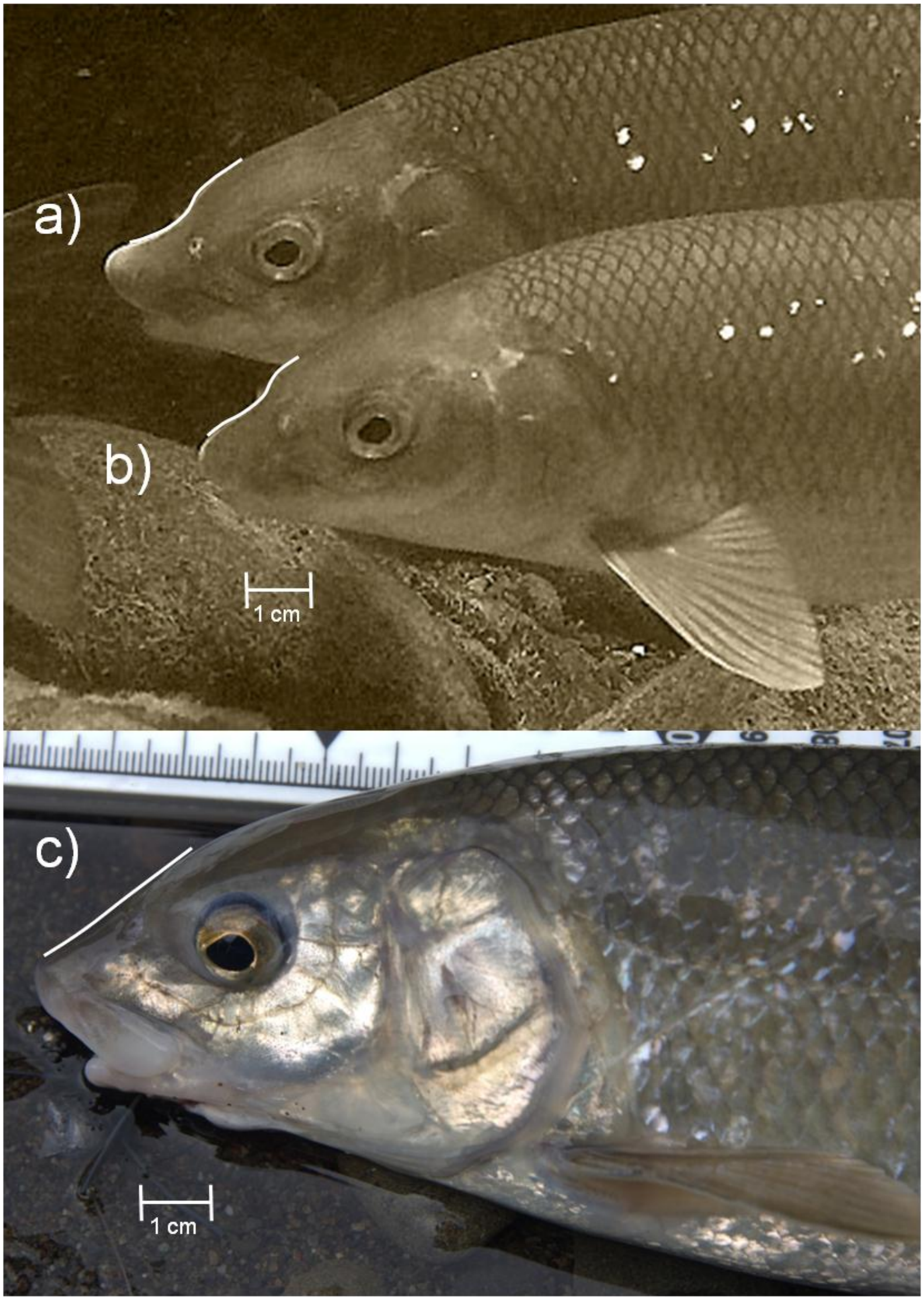

Figure 2. Mountain whitefish morphotypes in the Quileute basin, WA: pinocchio (a), intermediate (b), and normal (c). The thin white lines drawn over the snouts highlight differences between morphotypes.

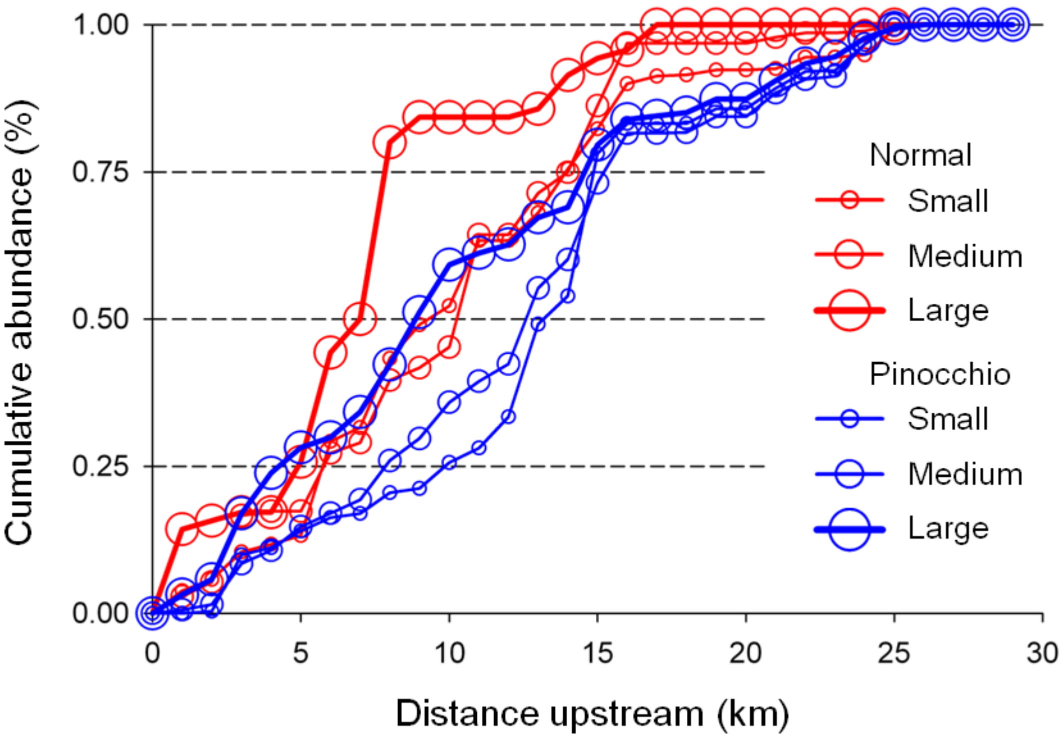

Figure 3. Cumulative abundance of mountain whitefish morphotypes and size classes versus distance upstream.

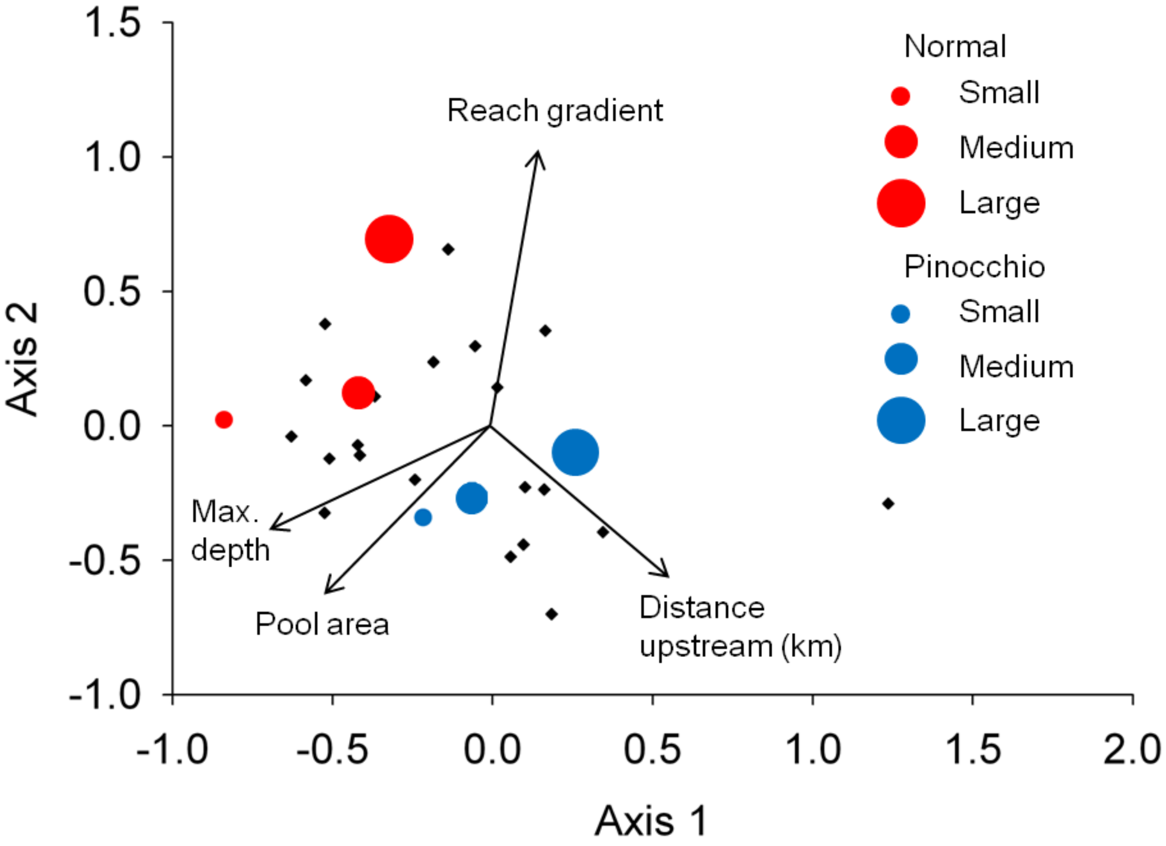

Figure 4. Non-metric multidimensional scaling (NMS) ordination of mountain whitefish morphotypes and size classes. Black diamonds represent 1-km bins in species space; blue and red symbols indicate the centroids (weighted average) of each size class. Vectors represent the loadings of environmental variables with respect to ordination axes.

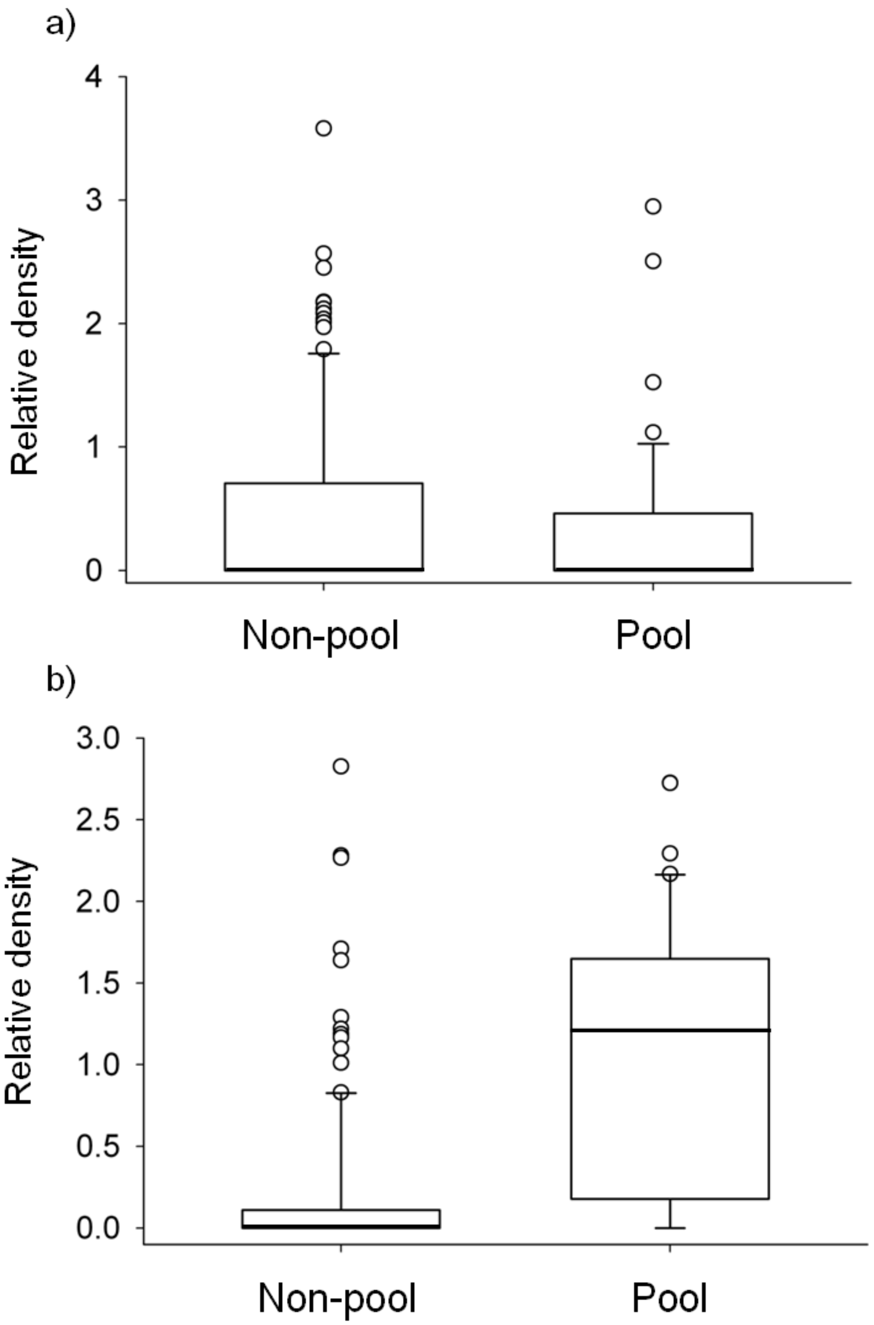

Figure 5. Differences in relative density (log-transformed) of normal (a) and pinocchio (b) mountain whitefish in non-pool (*n* = 124) and pool (*n* = 46) habitats in the mainstem and lower South Fork Calawah River. Top lines of boxes indicate the 75th percentile, the bottom lines indicate the 25th percentile, and the thick middle line indicates the median. Whiskers represent data that are no more than 1.5 times the inter-quartile range, and open circles are outliers.

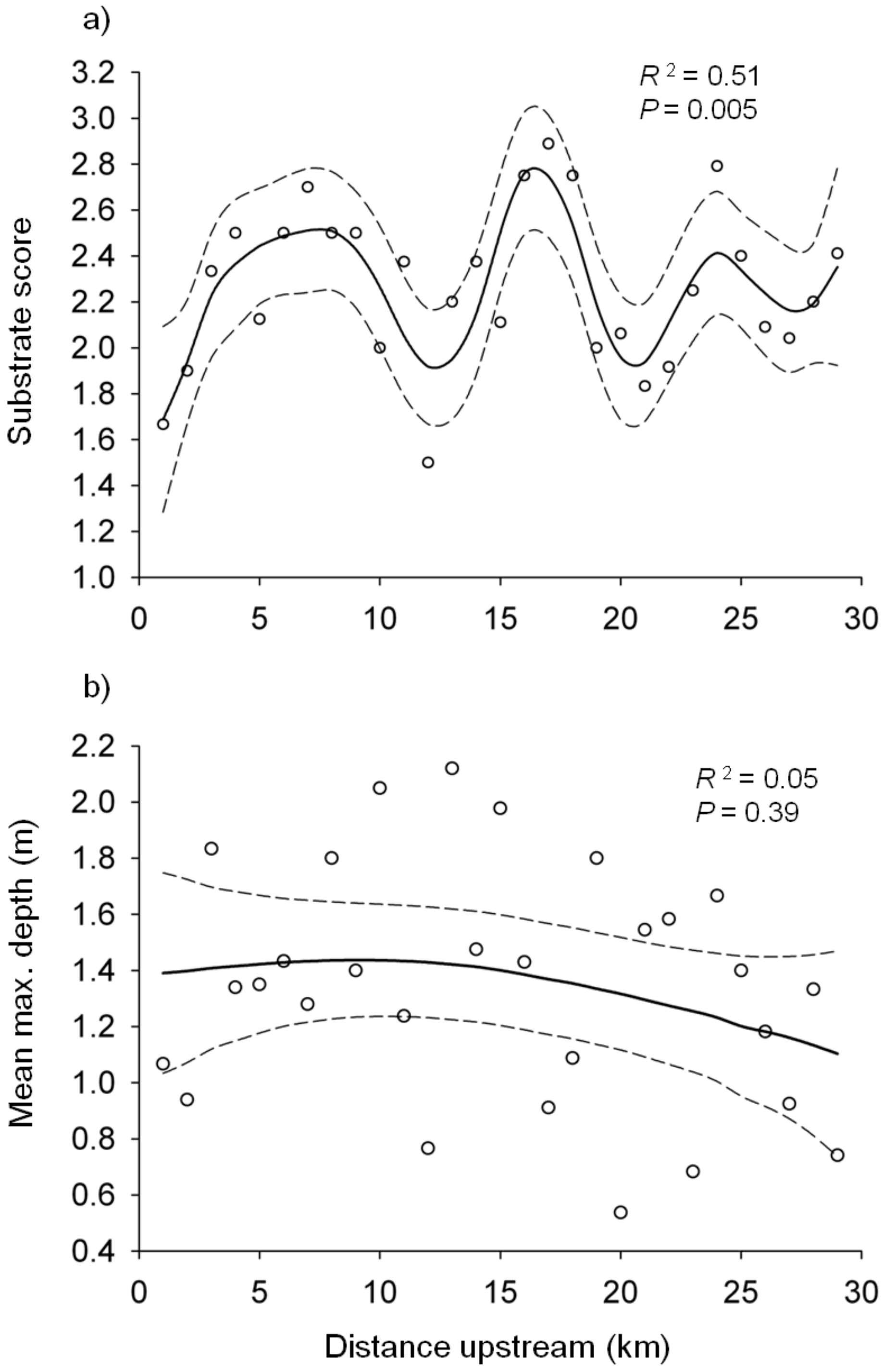

Figure 6. Thin-plate regression splines of spatial patterns in substrate score (a) and mean maximum depth (b). Substrate score corresponds to pebble, cobble, and boulder (i.e., scores of 1, 2, and 3, respectively). Dashed lines indicate ± 2 standard errors, open circles are observed values, and p-values refer to the significance of the smoothed parameter.

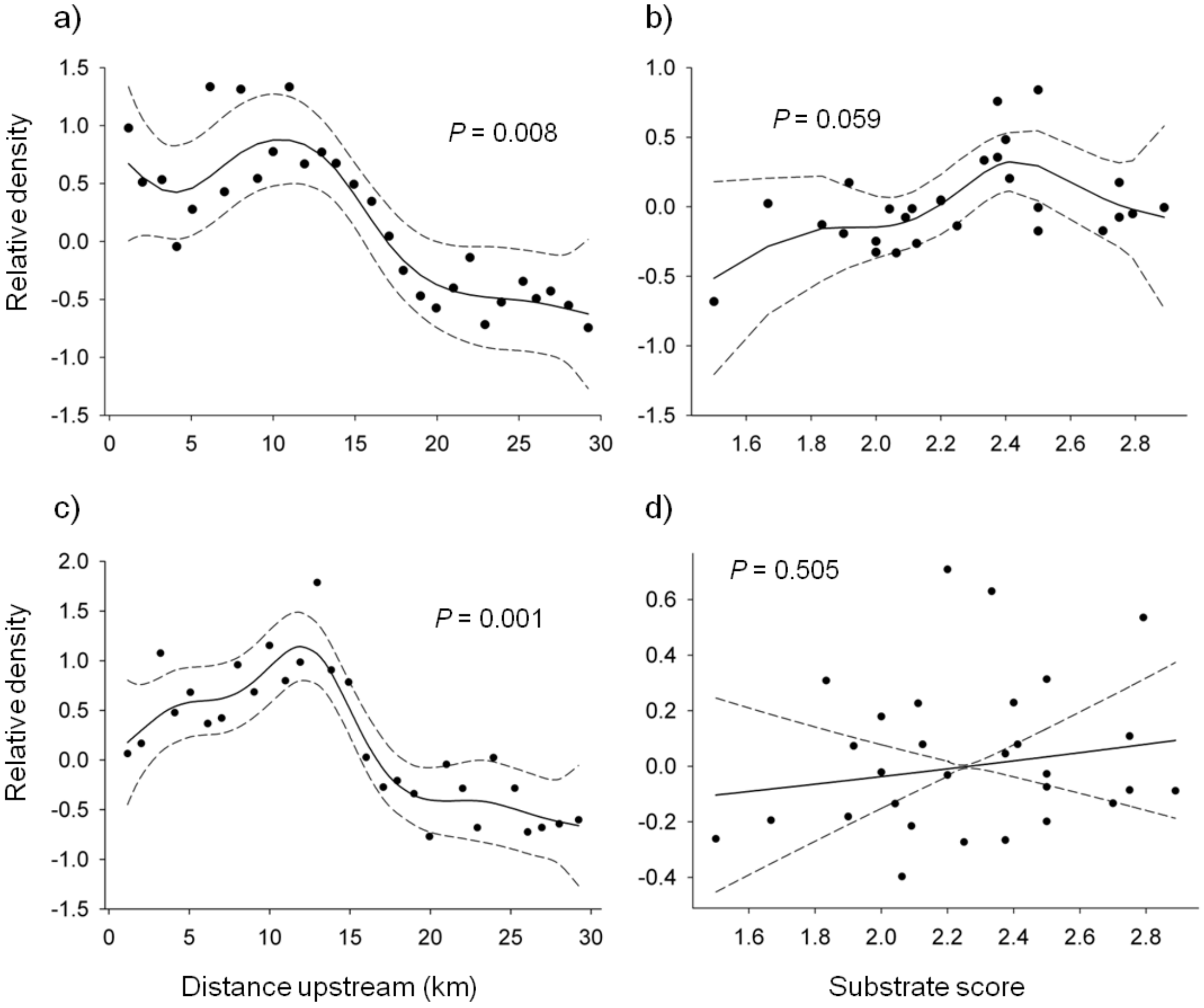

Figure 7. Thin-plate regression splines of modeled relative density of normal (a, b) and pinocchio (c, d) whitefish with respect to the additive effects of distance upstream and substrate score. Substrate score corresponds to pebble, cobble, and boulder (i.e., scores of 1, 2, and 3, respectively). Solid circles represent partial raw residuals, dashed lines indicate ± 2 standard errors, and p-values refer to the significance of the smoothed parameter.

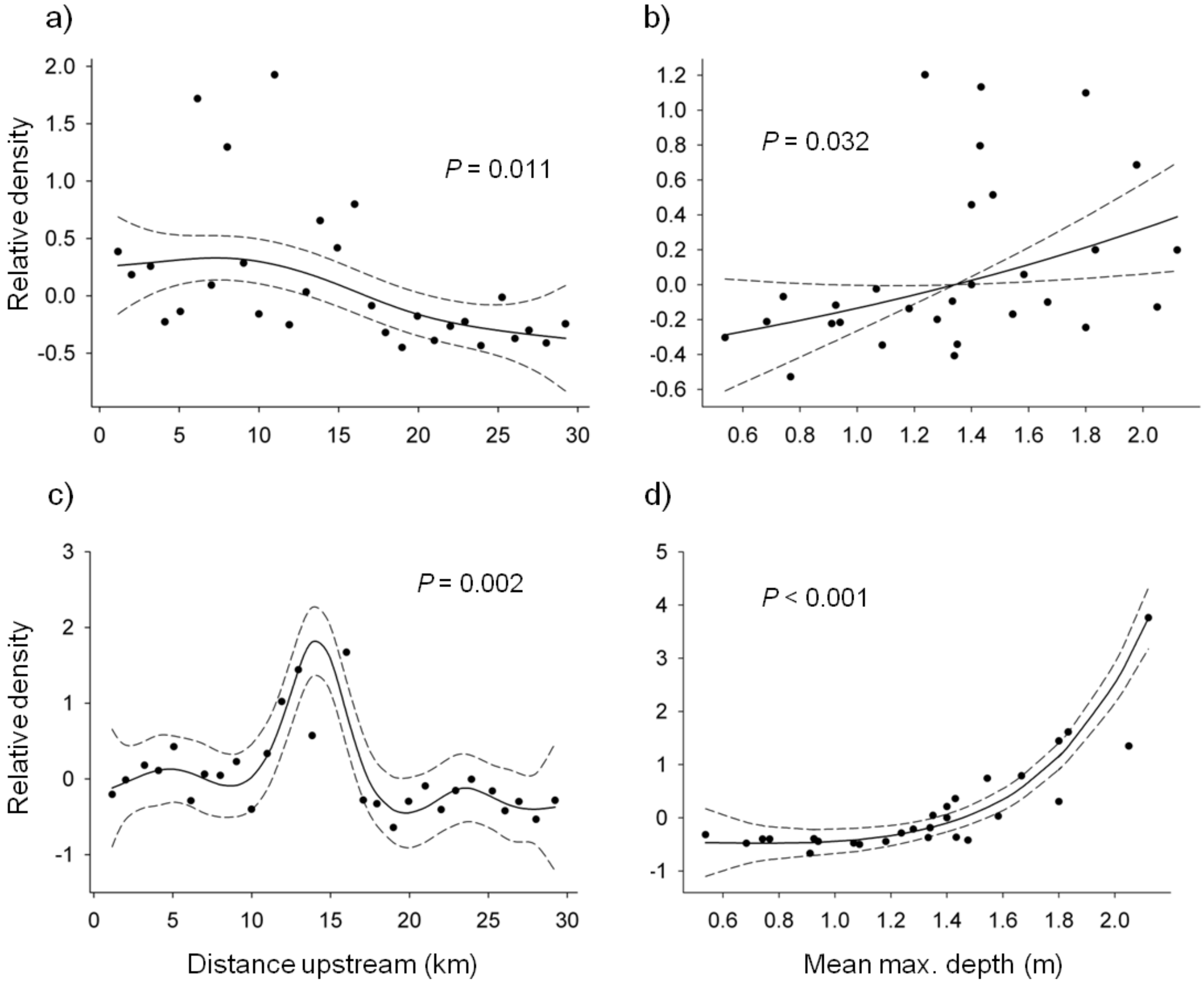

Figure 8. Thin-plate regression splines of modeled relative density of normal (a, b) and pinocchio (c, d) whitefish with respect to the additive effects of distance upstream and mean maximum depth. Solid circles represent partial raw residuals, dashed lines indicate ± 2 standard errors, and p-values refer to the significance of the smoothed parameter.

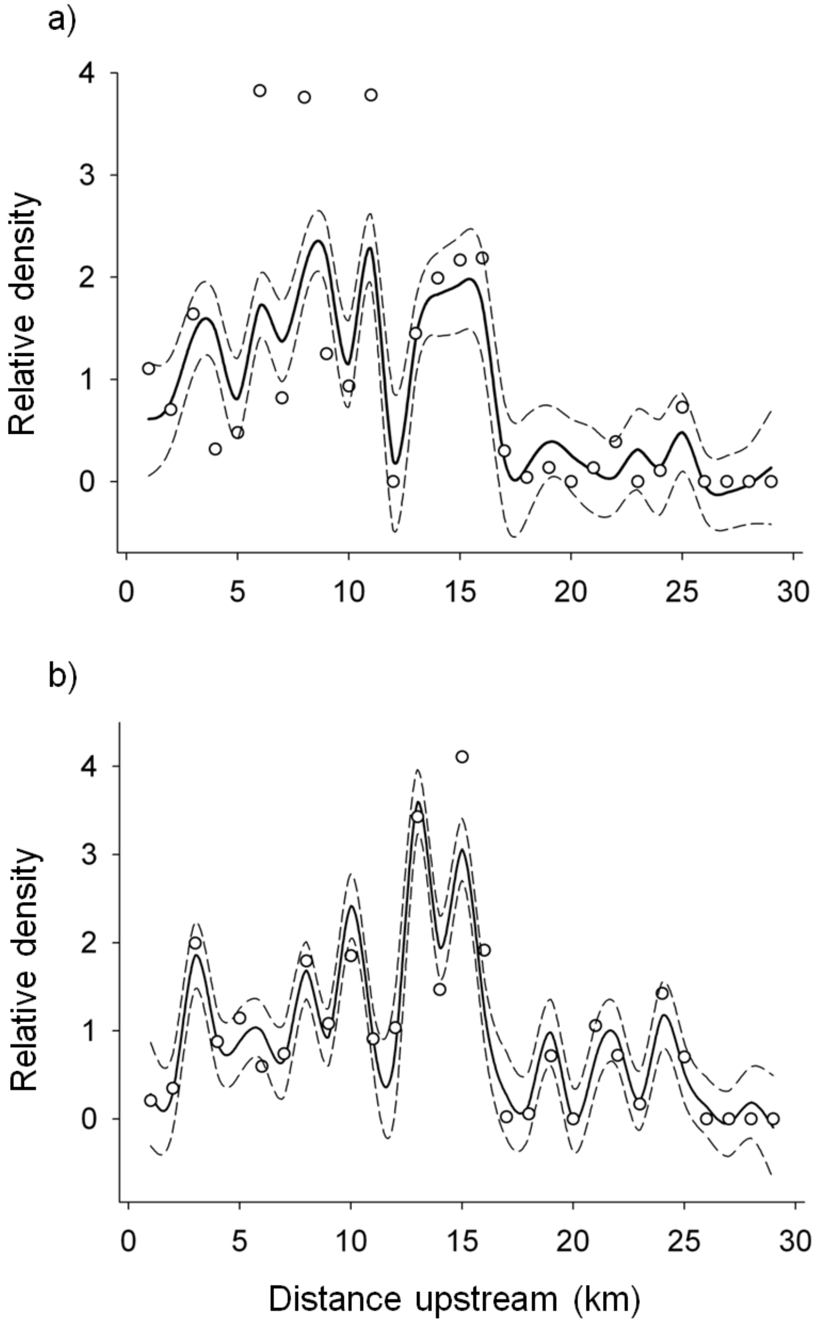

Figure 9. Longitudinal variation in modeled and observed relative density of normal (a) and pinocchio (b) mountain whitefish. The solid lines are locally weighted scatterplot smoothing (LOWESS) of the fitted values, dashed lines represent a LOWESS smooth of ± 2 standard errors, and open circles are observed values.

Table 1. Abundance and relative density of mountain whitefish (*Prosopium williamsoni*) by morphotype and size class in the Calawah River. See Equation 1 for the calculation of relative density.

Morphotype	Size class	Length (cm)	Raw abundance	Percent abundance	Mean relative density (± SD)
Normal mountain whitefish	Small	10-29	283	9	0.968 ± 1.396
	Medium	30-49	469	14	0.975 ± 1.167
	Large	≥ 50	70	2	0.986 ± 1.935
	All size classes		822	25	0.974 ± 1.192
Pinocchio mountain whitefish	Small	10-29	566	17	0.965 ± 1.420
	Medium	30-49	1542	47	0.980 ± 0.979
	Large	≥ 50	348	11	0.989 ± 0.907
	All size classes		2456	75	0.978 ± 1.004

Table 2. Summary statistics of physical habitat characteristics in the lower and upper mainstem Calawah River, and the lower and upper South Fork Calawah River. Sections were sampled at the unit-scale and data were binned into approximately 1-km reaches (*N* = 29) using major tributary junctions, and natural breaks in channel and unit type. Substrate score corresponds to pebble, cobble, and boulder (i.e., scores of 1, 2, and 3, respectively). Valley width index is the ratio of floodprone width to channel width.

Habitat characteristics	Lower mainstem (*n* = 10)			Upper mainstem (*n* = 6)			Lower South Fork (*n* = 9)			Upper South Fork (*n* = 4)		
	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
Length (km)	1.0	0.86-1.19	0.12	1.0	0.88-1.09	0.09	1.02	0.87-1.26	0.11	0.94	0.75-1.06	0.15
Channel width (m)	47	38-59	5.5	40	31-45	4.9	39	22-53	10.1	17.5	15-21	2.9
Channel type (%)												
Pool-riffle	52	0-100	39	44	0-100	50	0.37	0-100	39	27	0-54	25
Forced pool-riffle	30	0-100	33	17	0-100	41	41	0-100	40	57	13-100	37
Plane bed	17	0-54	23	40	0-100	49	22	0-100	44	16	0-44	21
Gradient (%)	1.2	0.02-1.5	0.04	1.2	0.09-1.5	0.03	1.2	0.08-2.2	0.05	1.1	1-1.4	0.02
Pool area (%)	35	0-76	23	37	24-54	12	29	0-66	29	23	11-44	16
Mean max. depth (m)	1.45	0.94-2.05	0.35	1.5	0.77-2.12	0.49	1.25	0.54-1.80	0.46	1.05	0.74-1.33	0.26
Substrate score	2.3	1.7-2.7	0.33	2.2	1.5-2.75	0.41	2.3	1.8-2.9	0.40	2.2	2.0-2.4	0.16
Valley width index	1.54	1.32-1.78	0.13	1.53	1.30-1.84	0.19	1.56	1.31-2.05	0.22	1.52	1.49-1.57	0.03

Table 3. Pearson correlation matrix of habitat variables. Values greater than 0.50 are in bold to highlight pairs that are likely to cause variance inflation in multiple regression due to multi-collinearity.

Variable	DU	P-R	F P-R	PB	GRA	CW	FP	VWI	POOL	DEP	SUB
P-R	0.28										
F P-R	0.32	**-0.56**									
PB	-0.03	**-0.50**	-0.44								
GRA	-0.11	-0.29	-0.25	**0.58**							
CW	**-0.71**	0.39	-0.40	0.00	0.04						
FP	**-0.68**	0.36	-0.41	0.04	0.12	**0.97**					
VWI	-0.02	-0.11	-0.21	0.34	0.49	0.11	0.32				
POOL	-0.05	-0.11	0.27	-0.17	**-0.71**	0.03	-0.03	-0.28			
DEP	-0.22	-0.15	0.23	-0.08	-0.46	0.20	0.16	-0.11	**0.70**		
SUB	0.05	**-0.63**	0.06	**0.62**	0.46	-0.10	-0.04	0.35	-0.04	0.08	
COV	-0.25	**-0.55**	-0.16	**0.76**	0.42	0.14	0.15	0.22	-0.04	0.17	**0.64**

Abbreviations: DU (distance upstream), P-R (% pool-riffle), F P-R (% forced pool-riffle), PB (% plane bed), GRA (% bin gradient), CW (channel width), FP (floodprone width), VWI (valley width index), POOL (% pool area), DEP (mean max depth), SUB (substrate score), and COV (% instream cover).

Table 4. Analysis of deviance and statistical parameters for generalized additive models (GAMs) predicting normal and pinocchio whitefish relative density using forward step-wise selection of covariates. Adjusted R^2 values for the overall model are shown for each morphotype, with residual deviance, marginal reduction in deviance, percent reduction of null deviance, and associated p-values.

Normal GAM (R^2 = 0.64)						Pinocchio GAM (R^2 = 0.87)					
Covariate	Effect d.f.	Residual deviance	Reduction in deviance	Percent reduction in deviance	*P*	Covariate	Effect d.f.	Residual deviance	Reduction in deviance	Percent reduction in deviance	*P*
Distance upstream	4.9	4.2	3.5	45.8		Mean max depth	2.9	1.9	3.9	66.9	
Substrate score	4.1	3.1	1.1	13.6	0.02	Distance upstream	7.3	0.5	1.4	24.4	0.0001
Bedrock occurrence	1	1.8	1.4	17.6	0.02						

Null d.f. = 28; normal whitefish GAM null deviance = 7.7; pinocchio whitefish GAM null deviance = 5.9.

Appendix A. Distribution of rainbow trout, cutthroat trout, and mountain whitefish size classes in the Calawah River, Washington, USA, during late spring to mid-summer 2010.

Introduction

The spatial distribution of stream salmonids may vary intra-annually according to different stream flows and temperature regimes (Schlosser 1991). Higher stream flow during spring run-off provides deeper channel units that may become unsuitable during summer base flow. I hypothesized that (1) higher stream flow during late spring would result in more available habitat, a less patchy distribution of salmonids (i.e., rainbow trout, cutthroat trout, and mountain whitefish), and greater overlap among species and size classes, and (2) that lower streamflow in August would result in a more patchy distribution and greater spatial segregation among salmonid species and size classes.

Methods

Extensive surveys (see *Visual surveys of fish and aquatic habitat*, pp. 7-8) in the Calawah River, Washington, were conducted in 2010 during late spring runoff (June 26 to July 2) when streamflow was approximately 7.5 m^3/sec^{-1}, and in mid-summer during base-flow conditions (August 16 to 19) when streamflow was approximately 1.8 m^3/sec^{-1}.

Results

The pattern of larger fish downstream was not apparent during the June survey and there was extensive overlap among all size classes of mountain whitefish, coastal cutthroat trout and rainbow/steelhead trout. In June, approximately 50% of the small rainbow trout were distributed throughout the lower 10 km of the mainstem Calawah River (Figure A1). In contrast, small rainbow trout were distributed much farther upstream, primarily in the South Fork Calawah River during the August survey (Figure A2). I enumerated 475 more small rainbow trout in August compared to June. Mountain whitefish outnumbered both trout species in all size classes, and small rainbow trout were more abundant than small cutthroat trout, which were the least abundant species overall (Table A1).

Discussion

Species and size classes of salmonids overlapped in June and were spatially segregated in August. It is likely that greater streamflow in June provided more habitat and allowed for vertical partitioning of species within channel units, thereby reducing both intraspecific competition among cohorts, and interspecific competition with small mountain whitefish and cutthroat trout for food and space (see Appendix B). Rainbow trout tend to feed higher in the water column than mountain whitefish (DosSantos 1985). Lower streamflow; thus, lower stage height may have restricted the ability of rainbow trout to occupy locations higher in the water column. In addition, the smaller body size of juvenile rainbow trout may potentially place them at a competitive disadvantage to larger bodied mountain whitefish (Jenkins 1969, Grand 1997, Hughes 1998). It is possible that interspecific interactions with mountain whitefish lead to the shift in the distribution of small rainbow trout farther upstream in August. The distribution of mountain whitefish was similar between the two sampling periods, and this may be a result of whitefish selecting summer feeding habitats prior to other salmonids. The distribution of coastal cutthroat trout, which is a “generalist” species, was also markedly similar between the two sampling periods. It is possible that cutthroat trout were able to occupy a variety of habitat types as conditions in the stream environment changed seasonally.

The abundance of small rainbow trout increased from June to August, and these results were unexpected due to the effects of predation and competition, which are typically greatest during summer months when low water levels reduce the amount of available habitat. It is possible that age 1+ rainbow migrated into the Calawah from other sub-basins due to competition for food and space. The Calawah River is one of four major sub-basins within the Quileute system (Sol Duc, Bogichiel, and Dicky Rivers), and whitefish are able to move freely throughout these basins. It is also possible that juvenile rainbow trout migrated downstream from headwater streams and tributaries as streamflow dropped during summer months. My surveys did not extend into the headwaters, so it was not possible to determine the amount of emigration from these area. Additional studies are needed to investigate the movement of juvenile rainbow trout in the Quileute system, and to elucidate how movement patterns are related to fitness and survival. My results highlight the importance of temporal variation in salmonid distribution, even over a short a time period (only six weeks in this case), and illustrate the need for data collected over a greater spatial and temporal extent.

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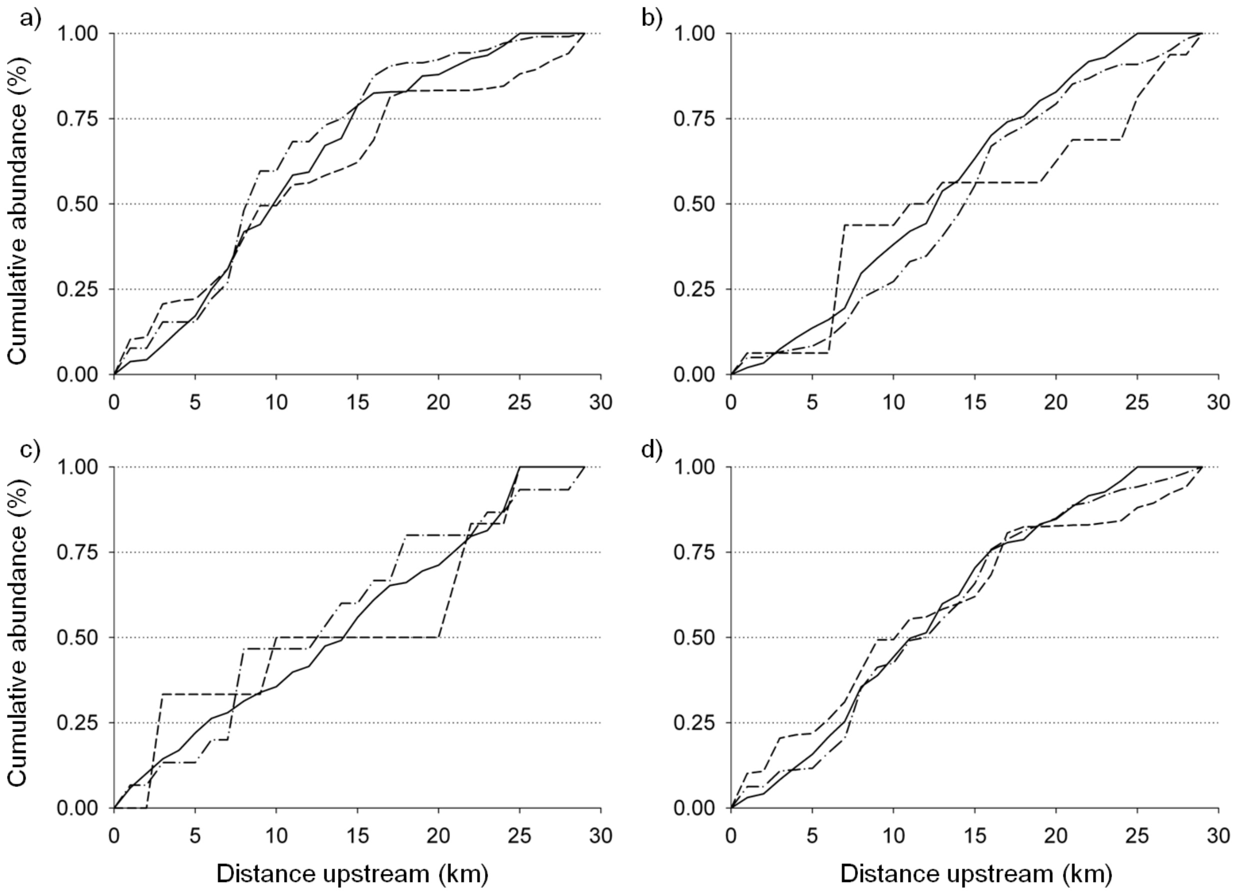

Figure A1. Cumulative abundance of mountain whitefish, rainbow trout, and cutthroat trout in June of small (a, 10-29 cm), medium (b, 30 – 49 cm), large (c, ≥ 50 cm), and all size classes (d). Solid black lines are mountain whitefish, dashed-dotted lines are coastal cutthroat trout, and dashed lines are rainbow/steelhead trout. Mountain whitefish morphotypes were not enumerated during the June survey.

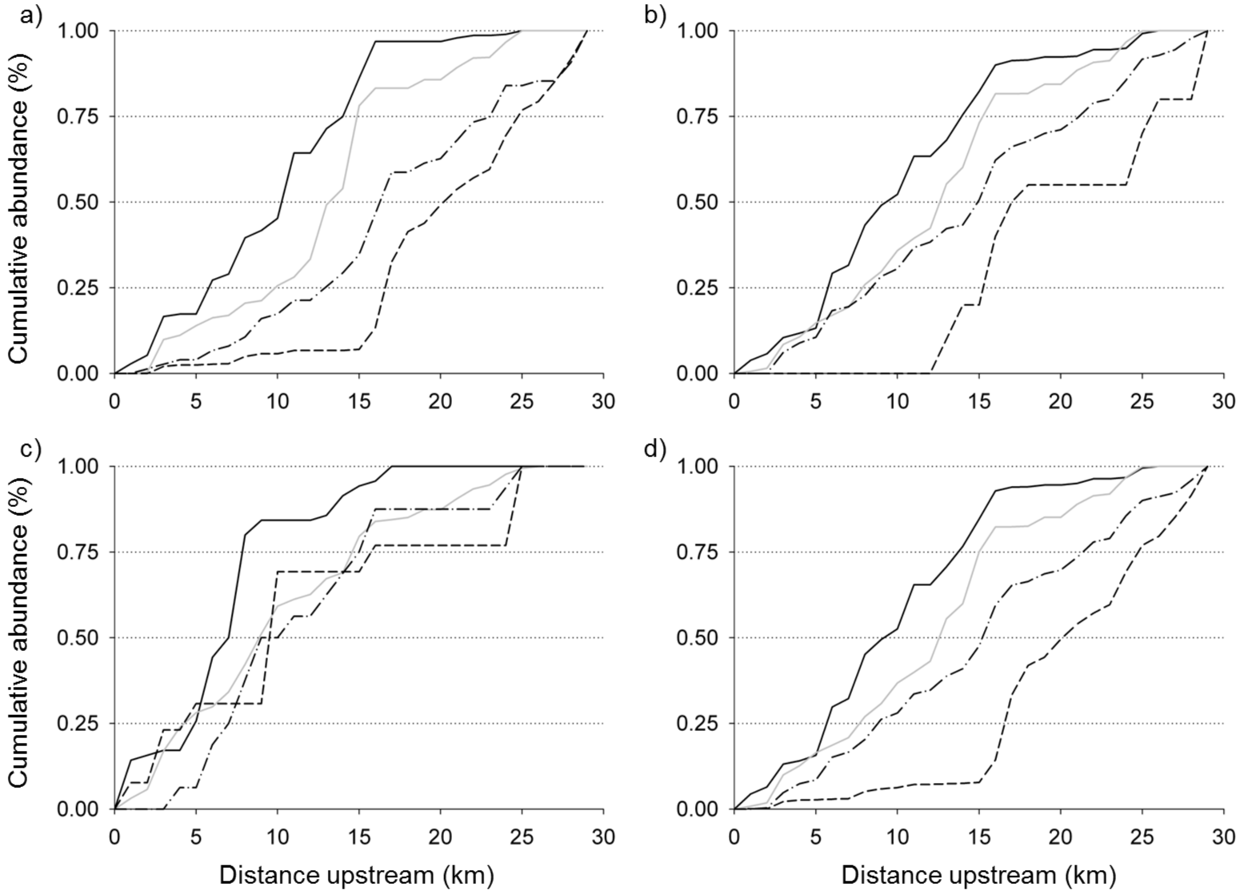

Figure A2. Cumulative abundance of mountain whitefish morphotypes, rainbow trout, and cutthroat trout in August of small (a, 10-29 cm), medium (b, 30 – 49 cm), large (c, ≥ 50 cm), and all size classes (d). Solid black lines are normal whitefish, grey lines are pinocchio whitefish, dashed-dotted lines are cutthroat trout, and dashed lines are rainbow/steelhead trout.

Table A1. Abundance of salmonids and respective size classes in June and August.

Month	Species	Small (10-29 cm)	Medium (30-49 cm)	Large (≥ 50 cm)	Total
June	Mountain whitefish	1159	1136	118	2413
	Rainbow/steelhead trout	867	16	6	889
	Coastal cutthroat trout	104	221	15	340
August	Mountain whitefish	849	2011	418	3278
	Rainbow/steelhead trout	1342	20	13	1375
	Coastal cutthroat trout	75	180	16	271

Appendix B. Observations on behavioral interactions among whitefish, rainbow and cutthroat trout in the Calawah River, Washington, USA.

Introduction

Mountain whitefish are often perceived by anglers and fisheries managers as competitors with resident trout (McHugh 1940, Sigler 1951). However, there is little evidence to support these perceptions. DosSantos (1985) found little overlap in diet between adult mountain whitefish and rainbow trout, although there was some evidence that whitefish competed with juvenile trout. No study has quantified behavioral interactions between trout and mountain whitefish.

Methods

I conducted intensive surveys of fish behavior in a stratified sample of channel units (pool, non-pool), in the mainstem Calawah River and South Fork Calawah River (n = 8). These sites were located 0.4 km, 1.2 km, 2.6 km, 3.3 km, 16.4 km, 18.2 km, 21.4 km, and 23.1 km upstream from the downstream initiation point of the extensive surveys. The intensive surveys of fish behavior began on July 12 and were completed on August 6, 2010. Each site was visited on one day, in the morning and afternoon, every two weeks. Upon entering the unit, I remained motionless for at least 5 minutes, allowing fish to acclimate to my presence. I held my position in the unit for 30 minutes during two time periods: the early morning (~ 08:00) and early afternoon (~ 13:00). If I did not observe any intraspecific or interspecific interactions among whitefish and trout in the first 15 minutes, I terminated the survey for that time period. Behavioral interactions were recorded in the following categories: head position, chasing, nipping, and biting. I also recorded information on fish size (see methods for extensive surveys) and species (including whitefish morphotype). I recorded dominant and sub-dominant social behavior between individual fish.

Results

Interactions among fish were more common in non-pool than in pool habitats, and intraspecific competition between small rainbow trout was more common than interspecific competition between rainbow and whitefish or cutthroat trout (Figures B1 and B2). Aggressive behavior, such as chasing, was more common among rainbow trout than among normal whitefish in non-pool habitat. Only one interspecific interaction was observed in pool habitats between a medium-sized (30-49 cm) cutthroat trout and a small (10-29 cm) rainbow trout. Large (≥ 50 cm) pinocchio whitefish in pools often maintained an upstream position in the feeding lane at the intersection of slow and fast water.

Discussion

Large whitefish dominated the majority of intraspecific interactions by upstream positioning in feeding lanes, and they were not challenged by smaller rainbow trout. Rainbow trout only chased similar-sized mountain whitefish that were not at the head of the feeding lane. Whitefish in riffles were also observed using their pectoral fins to maintain a position very close to the stream bottom and directly behind boulders where turbulence provided cover. Rainbow trout tended to feed higher in the water column and downstream of areas with high turbulence. These observations suggested that intraspecific competition may dominate rainbow trout behavior, and interactions with mountain whitefish may be limited to individuals that are similar in size. However, the sample size of my observations was very limited, and more study is needed to verify these results.

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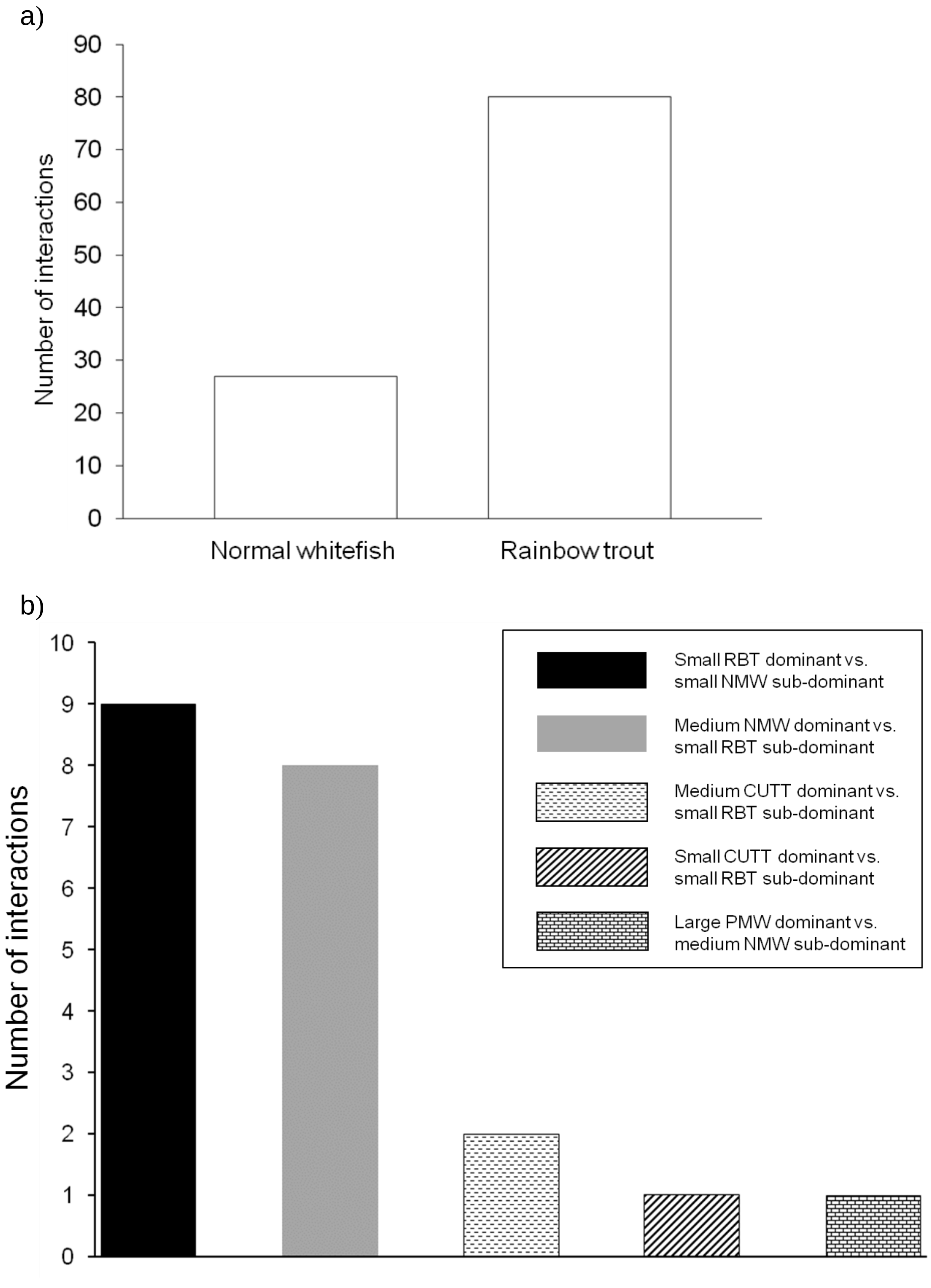

Figure B1. Intraspecific (a) and interspecific (b) interactions observed among mountain whitefish, cutthroat trout, and rainbow trout at the sub-unit scale in non-pool habitats. Abbreviations: NMW (normal whitefish), PMW (pinocchio whitefish), RBT (rainbow trout), CUTT (cutthroat trout).

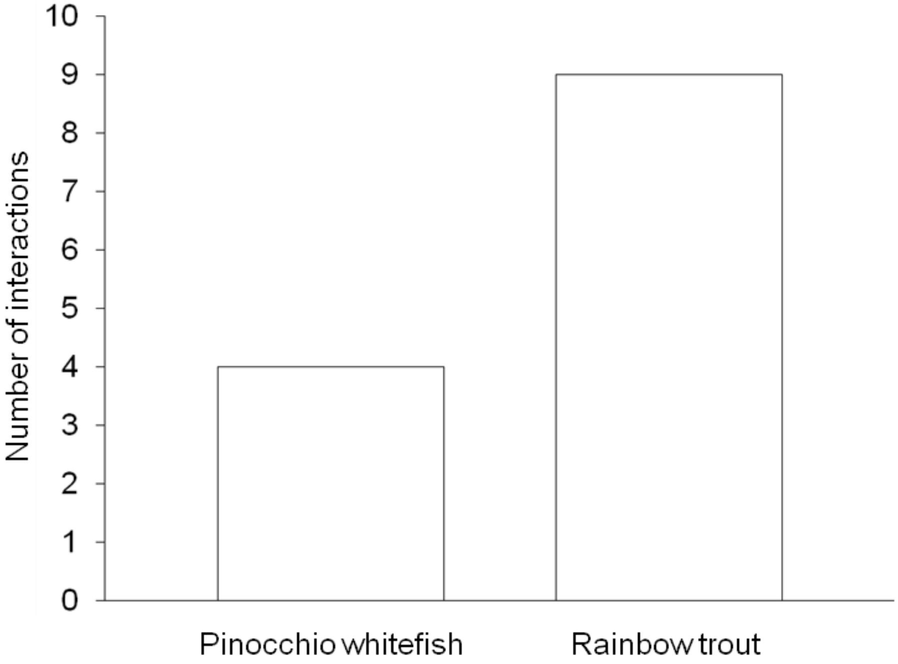

Figure B2. Intraspecific interactions observed among mountain whitefish and rainbow trout at the sub-unit scale in pool habitats.