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Seasonal microhabitat selectivity by juvenile steelhead in a central California coastal river

Robert W. Holmes*, Mark A. Allen, and Shannon Bros-Seeman

California Department of Fish and Wildlife, Water Branch, 830 "S" Street, Sacramento, CA 95811, USA (RWH)

Normandeau Environmental Consultants, 890 L Street, Arcata, CA 95521, USA (MAA)

San Jose State University, Department of Biological Sciences, San Jose, CA 95192, USA (SB-S)

**Correspondent: Robert.Holmes@wildlife.ca.gov*

Microhabitat data were collected at focal positions of juvenile steelhead trout *(Oncorhynchus mykiss)* in the Big Sur River, California during spring, summer, and fall. An equal-area sampling approach was used to guide fish surveys and allocate habitat availability sampling among seasons, river reaches, and mesohabitat types. Juvenile steelhead trout habitat selection changed with fish size, season, discharge, and habitat availability. Water depth and water velocity were of primary importance in habitat selection for all size groups of rearing steelhead. Habitat Suitability Criteria (HSC) were prepared for water depth, mean water velocity, focal velocity, specific escape cover types, and distance to in-water escape cover to reflect seasonal habitat selectivity for rearing steelhead. Habitat "preference" HSC (use adjusted for availability using the U/A forage ratio) were also developed and compared with the equal-area selectivity HSC and with habitat availability. The U/A results produced extreme shifts in maximum suitability for several curves, and perhaps more significantly the U/A ratios severely deflated suitabilities where the majority of the fish were observed. With proper habitat stratification and non-limiting sampling conditions (e.g., adequate flows and non-degraded habitat), use of an equal-area sampling design for site-specific selectivity HSC development was determined to be a viable option for development of biologically relevant and representative HSC, and apt for effective environmental flow recommendations.

Key words: forage ratio, habitat selection, HSC, microhabitat, *Oncorhynchus mykiss*, preference, selectivity, steelhead trout

Habitat suitability criteria (HSC) are an integral biological component of an instream flow-regime needs assessment (Bovee et al. 1998; Annear et al. 2004). HSC are typically developed within the framework of the Instream Flow Incremental Methodology (IFIM) decision-making approach (Bovee et al. 1998), and then can be used through various applications to link the species and life stage(s) of interest to their physical environment. One- and two-dimensional hydraulic habitat models (Milhous et al. 1989, Waddle et al. 2000) are two such applications commonly employed to evaluate stream flow and habitat relationships for salmonids. Within the context of the IFIM, HSC are indices of characteristic behavioral traits of a species that are established as standards for comparison to modeled habitat conditions (Bovee 1986). Biologically accurate and relevant HSC are required for the models to accurately predict and reflect how the quantity and quality of habitat changes under different flow regimes (Parsons and Hubert 1988, Beecher et al. 2002).

HSC development relies on an unbiased stratified sampling strategy that reflects the spatial or temporal changes of habitat use patterns of the target species. Mesohabitat components (i.e., pools, riffles, runs, glides) typically guide the broader sampling for development of riverine HSC. Microhabitat variables, such as water depth, water velocity, cover, and substrate are the most common variables used in the development of HSC. These microhabitat variables influence the use of local stream habitats by the target species and their respective life stages, and their availability varies with flow. The range of suitability for each microhabitat variable is between 0.0 (unusable) and 1.0 (optimal; Bovee and Cochnauer 1977).

HSC curves can be developed by various levels of rigor from strictly professional judgment with no actual field data or validation for the species, life stage, or river of interest, to being developed from site-specific field observations of habitat use. Developing site-specific HSC involves collecting data from locations where target fish are observed or captured (e.g., habitat "utilization" data). To avoid bias, the habitat utilization data must account for the effects of habitat availability on fish habitat selection (Bovee 1986). Two methods commonly employed to account for effects of habitat availability include equal-area sampling, a design-based protocol (Thomas and Bovee 1993, Bovee et al. 1998, Allen 2000), and application of the forage ratio formula (Johnson 1980, Voos 1981) based upon the concept of food electivity (Ivlev 1961), a mathematical adjustment of utilization data by availability data to arrive at an estimate of a fish's habitat "preference" (Bovee 1986, Moyle and Baltz 1985, Beecher et al. 1993, Beecher et al. 1995). Other protocols for developing HSC that attempt to account for habitat availability include density sampling (Rubin et al. 1991, Aadland and Kuitunen 2006), and presence-absence sampling (Thielke 1985, McHugh and Budy 2004, Gard 2010).

Use of an equal-area sampling approach to directly account for habitat availability (Bovee et al. 1998) is more recently referred to as representing target organism "selection" (Manly et al. 2002), hereafter referred to as "selectivity." Although use of the terms "preference" and "selectivity" may seem a matter of semantics, there are broader concerns for HSC development, application, and associated biological representativeness and relevance for the target species. For example, a primary limitation of developing "preference" HSC using the forage ratio is that the mathematical adjustments for limited habitat availability may sometimes result in overcorrected HSC (Bovee et al. 1998), particularly if applied when habitat availability is not limited (Hayes and Jowett 1994). Such instances could lead to biased HSC and environmental flow recommendations that are insufficient for maintaining a robust population, or else recommendations for more water than what is naturally available.

Recurring drought conditions in California underscore the need for accurate and reliable tools to inform streamflow management decisions. Despite being an essential component of many types of flow management modeling tools, steelhead trout (*Oncorhynchus mykiss*) HSC are not available for small California coastal rivers. Further, California's South-Central Coast (SCC) steelhead trout Evolutionary Significant Unit (ESU) populations have declined from about 25,000 spawning adults per year to fewer than 500 (NMFS 2007). The free-flowing Big Sur River is thought to represent an important source population for the South-Central steelhead trout ESU that may help maintain some of the other very small populations that occur throughout the Big Sur Coast. Furthermore, the Big Sur River is considered a steelhead trout stronghold (Wild Salmon Center 2010) and, as such, a candidate coastal river for development of steelhead trout HSC.

The primary objective of this study was to investigate seasonal microhabitat selectivity by juvenile steelhead trout in a relatively pristine, unregulated coastal stream, and to fill a significant data gap in California-based steelhead trout literature. This information is critically important for designing studies to assess habitat suitability in California, where conflicts over limited water supplies are ever-increasing. Further, existing HSC data for steelhead trout in California are based on large, regulated rivers in interior California, where the application and biological relevance of those criteria to smaller coastal streams is uncertain. HSC developed from a mostly unaltered, coastal stream should help to avoid the potential biases from application of non-local HSC developed from rivers with altered flow and habitat conditions. A secondary objective was to develop, and compare and contrast HSC using two common methods intended to account for habitat availability: a design-based sampling approach (equal-area sampling) either with or without a mathematical adjustment using the forage ratio. Both methodologies are commonly employed in HSC studies, and both have strengths and weaknesses that must be considered during development and application.

The management applications of this investigation, in addition to filling a significant HSC data gap for coastal steelhead trout near the southern extent of their distribution, include developing an improved understanding of juvenile steelhead trout behavior and habitat selection in an unimpaired river system. An understanding of juvenile steelhead trout habitat selection from an unregulated coastal stream is important for designing habitat restoration efforts and identifying restoration priorities in other coastal streams that may have altered flow regimes or degraded habitat conditions, or both. Further, the HSC used in some IFIMs may originate from other studies because the stream under investigation is not a good source stream for site-specific HSC development. In such cases, assurances that the HSC are not biased by flow regulation or other habitat and sampling limitations is important in evaluating the transferability (Thomas and Bovee 1993) of those data between streams.

Materials and Methods

Study area.—The Big Sur River is located in southern Monterey County, California (Figure 1) and has a watershed of approximately 155 km^2 with no major dams, diversions, or reservoirs. The Big Sur River, which has limited access, originates in the steep canyons of California's Ventana Wilderness within the Los Padres National Forest, and flows northwesterly through federal and private lands, two state parks (Pfeiffer Big Sur and Andrew Molera), and a small lagoon before joining the Pacific Ocean about 4.5 km southeast of Point Sur. Significant tributaries include Pfeiffer-Redwood Creek, Juan Higuera Creek, Post Creek, and Pheneger Creek.

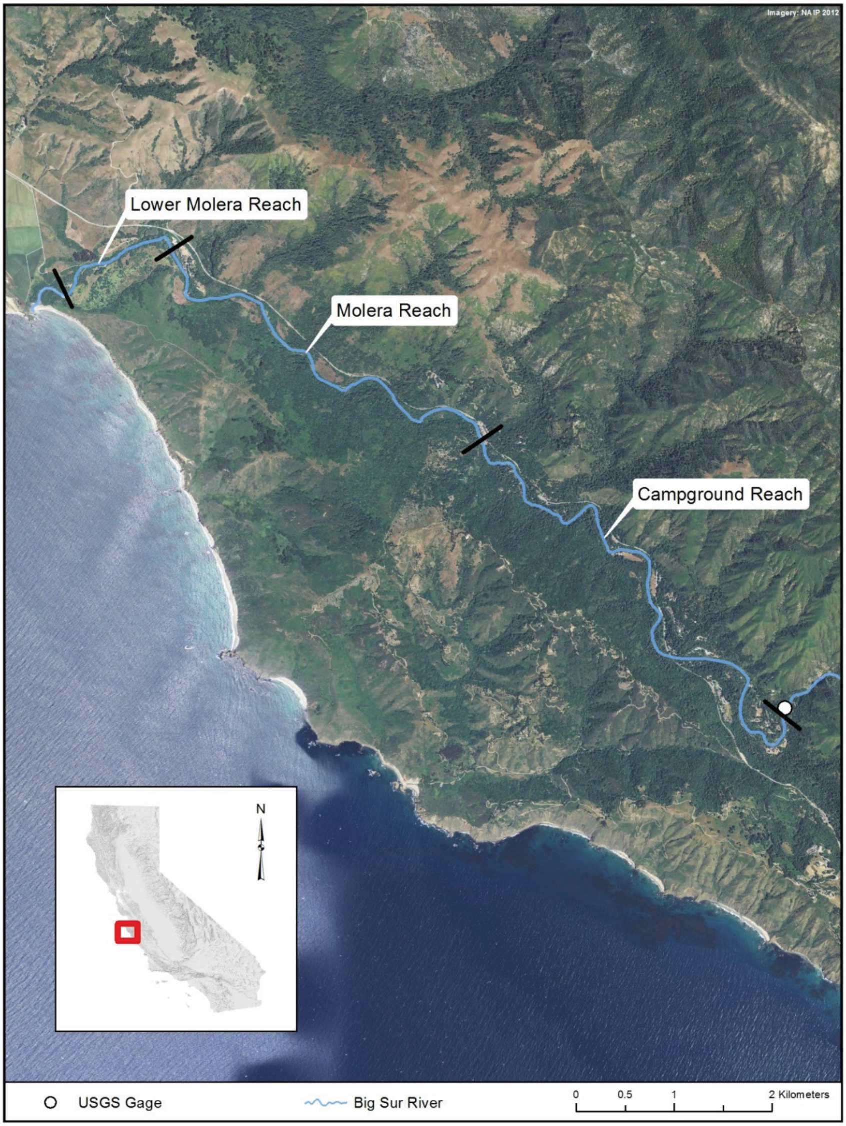

FIGURE 1.—Map of study reaches referenced in this paper along the Big Sur River, Monterey County, California.

The hydrology of the Big Sur River is typical of many coastal California rivers, experiencing high winter flows, low summer flows, and variable annual discharges. Most of the annual flow occurs in the winter with stream discharge reflecting local and watershed-wide rainfall patterns. Flows in winter may rise and recede rapidly in association with rainfall events, while flows in the summer tend to be more stable and predictable as they recede into the fall months.

Percent exceedance flows are typically used as a guideline for describing the watershed hydrology, as well as for making informed decisions about water resources planning and management. The percent exceedance flows between 20 and 80 percent reflect the most commonly observed flows in the stream, with the 50 percent exceedance flow reflecting the stream's natural benchmark. The 20, 50, and 80 percent exceedance flows for the Big Sur River are 2.83, 0.82, and 0.39 m^3/s, respectively. The Big Sur River is predominately a single-salmonid species river, where steelhead trout use the study area year-round for migration, spawning, incubation, rearing, or emigration, or all of these. Further, the Big Sur River is free-flowing, in relatively pristine condition with limited anthropogenic impact.

Sampling strategy.—Sampling effort was stratified by season, reach, study site, and mesohabitat type. Seasonal stratification was important to reflect juvenile steelhead trout life-history characteristics during the rearing period on a coastal stream and how they may change as the fish grow during this period. The study area includes three reaches (i.e., Lower Molera, Molera, and Campground), each representing generally homogenous stream segments based upon gradient, geomorphology, hydrology, riparian zone type, flow accretion, and channel metrics (Figure 1). The reaches extend approximately 12 km from the lower-most part of the river at the lagoon-river transition upstream to Pfeiffer Big Sur State Park near USGS gage 11143000.

Summer sampling took place in June 2010 in the Lower Molera Reach, and in August 2010 in the Molera and Campground reaches. The survey (fish use) data were combined to reflect the equal area sampling design and represent juvenile steelhead trout microhabitat distributions during the summer time period. Fall sampling took place in all three reaches during October 2010 and represents the fall time period for rearing juvenile steelhead trout. Sampling resumed in May 2012 on all reaches to identify fry microhabitat distributions during spring.

Mesohabitat classification consisted of partitioning the reaches into low-gradient riffle, pool, glide, run (and shallow run) mesohabitat types (Flosi et al. 2010). Study sites were selected using a stratified random sampling design. First, each study reach was partitioned into three approximately equal sub-reaches based upon the number of mesohabitat units. A study site was then randomly selected in the lower third, middle third, and upper third of each sub-reach. This process was repeated until each sub-reach contained one of each mesohabitat type. Additional mesohabitat units, beyond the initial random draw, were also randomly selected from each reach or mesohabitat type stratum if needed to achieve equal-area (i.e., square meter) sampling and adequate sample numbers of fish (Bovee et al. 1998).

The equal-area sampling approach was intended to account for the influence of habitat availability on fish selectivity by sampling the same surface area of mesohabitats composed of different depths and velocities, then allowing the relative density of observations in each microhabitat to dictate the shape of the final HSC curve (Thomas and Bovee 1993, Allen 2000). The Big Sur River was not intensively mapped into discrete cells of specified depth or velocity categories; instead we opted to utilize a more simplified and rapid approach that associated conventional mesohabitat types with combinations of depth and velocity. For example, pools can generally be characterized as having an abundance of deep and slow microhabitats, whereas riffles are dominated by shallow and fast microhabitats. In like manner, runs are relatively deep and fast, whereas glides are comparatively shallow and slow. These four mesohabitat types thus approximate the four combinations of depth and velocity, and were the basis for the equal-area sampling design within the mesohabitat stratum.

Although pools also contain shallow depths along their margins, and slow velocities may occur near the banks of riffles, if a fish demonstrates a true preference for deep and slow habitat, it will likely occur at highest densities in the deeper and slower portion of the pool (i.e., not along the shallow margins). Likewise, a fish preferring fast velocities will occur most often in the swifter portions of a riffle or run, not in the calmer margin areas. If each of these mesohabitats is sampled at equal intensity, combining the target species or lifestage depth and velocity measurements among the mesohabitats will yield an HSC curve that represents its habitat selectivity by virtue of the density of observations in deep, shallow, fast, or slow microhabitats.

Fish observation techniques.—We sampled for steelhead trout fry (<6 cm) and juvenile (6-9 cm and 10-15 cm) life stages during three seasons (summer, fall, and spring). Habitat use data were collected for all undisturbed steelhead observed via direct underwater observation. Potential diving scenarios for collecting HSC data depended upon (1) fry/juvenile densities; (2) water clarity; and (3) channel width. Where narrow channel widths and adequate water visibilities allowed, a single diver collected HSC data with support from a data recorder. Where channel widths prevented a single diver from fully covering the entire sampling area, two divers or more worked upstream together, communicating to avoid replicate observations. Each diver transferred HSC data to one or two data recorders.

Water visibility was estimated using an 8-cm juvenile trout rapala. The recorder would suspend the rapala mid-depth in the water column using a sinker and monofilament line. The snorkeler would move away from the rapala until they were as far away as possible while still being able to see color markings on the rapala. Visibility was determined to be the maximum distance the underwater observer could see the rapala and color markings.

In each sampling (mesohabitat) site, the observers entered the water about 6 m downstream of the site, and moved slowly upstream through the site, observing steelhead and determining their focal positions. Location markers (weights with numbered flags) were placed where undisturbed steelhead (1 or more) were observed. Where large groups (>20 individuals) of fry or other juveniles were distributed over a larger (0.30 m^2) area that encompassed different water depths and velocities, they received several measurements that were treated as individual observations to characterize the different microhabitats and different sizes of fish within the groups.

Divers attempted to move around, rather than move through, fish positions to avoid herding fish within or out of the site. Fish that were disturbed by the diver prior to identification of the fish's focal position were not marked, but were noted as present and not included in subsequent analyses. Fish marker number, number of fish, estimated size (fork length[s] to nearest cm for each fish by reference to an underwater ruler), fish activity (e.g., holding, feeding), and focal height (i.e., actual distance above the substrate or relative height in the water column) were recorded for each observation. A numbered marker was placed underneath individual fish or sub-group focal position and the data were transmitted to the nearby data recorder. The observer then proceeded upstream and marked all undisturbed fish in the sampling unit.

After the dive was completed, habitat characteristics were measured at all observation markers. Habitat characteristics recorded for each marked fish location were: water depth, mean column water velocity (mean velocity), focal velocity, overhead cover (in-water and out-of-water cover type) presence, distance to escape cover, and distance to bank (Table 1). Escape cover was defined as any object capable of concealing a juvenile steelhead from aquatic or terrestrial predators, including unembedded cobbles and boulders, woody debris, instream branches, or overhead branches within 46 cm of the water surface. When multiple cover types were present at a fish focal position, the object type possessing the greatest concealment opportunity for a fish was recorded. Distance to that cover object was then measured to the nearest 1.5 cm; cover objects >3.1 m from a focal position were considered no cover. Water depth was measured with a graduated top-setting rod to nearest 30.5 mm. Velocity was measured with a Marsh McBirney electromagnetic water velocity meter to the nearest 3.0 mm/sec following standard U.S. Geological Survey procedures (Rantz 1982). River stage was monitored to assess potential changes in stage during the surveys using USGS 11143000 and USGS 11143010.

Table 1.—Vegetative codes and substrate codes referencing environmental conditions associated with the Big Sur River, Monterey County, California.

	Vegetative Codes		Substrate Codes	Size (cm)
0	None	20	None	
1	Filamentous algae	21	Clay	
2	Non-emergent rooted aquatic vegetation	22	Sand or silt/sand	< 0.25
3	Emergent rooted aquatic vegetation	23	Coarse sand/DG	0.25-0.5
4	Grass	24	Small gravel	0.5-2.5
5	Sedges/rushes	25	Medium gravel	2.5-5
6	Vines/ poison oak	26	Large gravel	5-7.6
7	Branches &/or small vegetation < 10 cm, IW	27	Gravel/cobble	7.6-10
8	Branches &/or small vegetation < 10 cm, OW	28	Small cobble	10-15.3
9	Branches > 10 cm, IW	29	Medium cobble	15.3-23
10	Branches > 10 cm, OW	30	Large cobble	23-30
11	Tree trunks < 10 cm dbh, IW	31	Small boulder	30-61
12	Tree trunks < 10 cm dbh, OW	32	Medium boulder	61-122
13	Tree trunks > 10 cm dbh, IW	33	Large boulder	>122
14	Tree trunks > 10 cm dbh, OW	34	Bedrock	
15	Roots and root-wads	35	Undercut bank	
16	Shrubs < 10 cm			
17	Duff, leaf litter, organic debris			
18	Small woody debris (< 10 cm), dead			
19	Large woody debris (> 10 cm), dead			

Habitat availability techniques.—Habitat availability data were collected in each sampled mesohabitat unit during each seasonal sampling event immediately upon conclusion of fish observation and data collection. Field procedures followed a random point sampling design that consisted of (a) random selection of cross-sectional transects, and then (b) random selection of measurement points along each transect. To keep the level of effort for habitat availability data consistent with the effort for fish habitat selection data (i.e., according to the equal-effort design), the number of availability measurement points in each sampled habitat unit was roughly proportional to the size of that habitat unit (e.g., larger individual mesohabitat units have more availability points than smaller units, but the overall number of availability points were equal among the mesohabitat types). This design provided a minimum of three habitat availability measurements from each of two to six transects per sampling unit. The total number of measurements per unit was based on unit size in order to maintain an equal effort in both the habitat availability and the fish habitat use datasets.

A second set of habitat availability measurements were also obtained from survey data collected from 118 transects spanning the three-reach study area in 2011. The transect locations were selected through a stratified random process to be used as part of a one-dimensional (1D) physical habitat hydraulic model analysis (Bovee 1997). The 1D data were based upon proportional, not equal, area habitat representation for hydraulic habitat modeling and are useful for comparisons with the habitat availability data collected in conjunction with the fish surveys.

HSC development.—Separate HSC were developed for each size class (e.g., <6 cm, 6-9 cm, 10-15 cm) and each seasonal period, and data were pooled among reaches and mesohabitat types in order to produce more generalized HSC representing the entire anadromous reach of the Big Sur River. Data were compiled into frequency histograms using bin size intervals of 0.03 m for water depth, and 3.0 cm/s for mean water and focal water velocity, respectively. The spring sample event was elected to identify rearing microhabitat selectivity for <6 cm steelhead fry, which represent the steelhead size class most representative of spring young-of-year rearing conditions. The summer and fall sampling events were elected to identify rearing microhabitat selectivity for larger juvenile steelhead in the 6-9 cm and 10-15 cm size groups.

Kernel-smoothing techniques (Jowett 2002, Jowett and Davey 2007) were used to develop HSC curves from the frequency of habitat selectivity, habitat availability, and preference (U/A) HSC curves, using the curve-fitting component of System for Environmental Flow Analysis (SEFA), an instream flow modeling toolkit (Payne and Jowett 2012). All smoothed curves were standardized by dividing them by their maximum values to provide suitability indices ranging from 0 to 1. For depth, some practitioners choose to subjectively maintain suitability at 0.5, 1.0, or at some intermediate value for depths beyond the last observation; we chose to maintain suitability at the value from the last observation into deeper water.

To further evaluate the representativeness of the equal-area selectivity HSC curves and the potential effects of habitat availability on these curves, alternative HSC curves were derived using the U/A forage ratio methodology. While the equal-area HSC are intended to reflect habitat selectivity (i.e., habitat choice) by the fish, the forage ratio criteria (Moyle and Baltz 1985) are also intended to reflect fish "preference," or habitat use adjusted for habitat availability (i.e., U/A). The U/A forage ratio is the proportion of habitat of a particular microhabitat category (e.g., water depths between 0.3 meters and 0.34 meters) selected by a fish, divided by the proportion of habitat units of that category available (Manly et al. 2002). Smoothed preference HSC were calculated within SEFA using the forage ratio formula as outlined and described by Jowett and Davey (2007).

Statistical analyses.—Statistical analyses assessed whether habitat availability differed from the habitat characteristics where fish were observed (habitat selected). Separate two-way for steelhead <6 cm and three-way Analysis of Variance (ANOVA) tests for larger juveniles (6-9 cm, and 10-15 cm) were conducted for each of the fish length classes. The factors in the statistical analysis were depth and velocity selection (fish habitat use, habitat available), mesohabitat (runs, riffles, pools and glides) and sample period (spring, summer, and fall for 6-9 cm fish, summer and fall only for 10-15 cm fish). Fish <6 cm were only abundant in the spring so sample period was not assessed. Significant effects ($P<0.05$) associated with selection (habitat used vs. habitat available) would indicate habitat selectivity. Holmes et al. (2014) outlined the complete statistical analyses of habitat use variables other than depth and velocity (i.e., fish focal velocity, fish focal position, overhead cover, escape cover distance, distance to bank).

Results

Approximately equal areas of mesohabitat types were sampled in each reach and season (Table 2). Steelhead trout were observed in all the mesohabitat types sampled in all seasons. Flows during sampling ranged from 0.99-1.44, 0.88-1.76, and 0.65-0.74 m^3/s for the spring, summer, and fall sample periods, respectively. Water visibility ranged from 2.7-6.0 m (mean 4.7 m). Water temperature ranged from 10-18°C with means of 15°C, 16°C, and 14°C for spring, summer, and fall, respectively. River stage did not change during each site survey.

Table 2.—Summary of total area sampled and total number of juvenile steelhead trout observed among mesohabitat types in the Lower Molera, Molera, and Campground reaches of the Big Sur River, Monterey County, California in 2010 and 2012. Sampling flows and corresponding monthly exceedance probabilities are outlined for each season.

Habitat Type	Spring 2012 Area (m^2)/Fish	Summer 2010 Area (m^2)/Fish	Fall 2010 Area (m^2)/Fish
Lower Molera Reach			
RUN	2,000/85	1,632/74	1,592/113
LGR	1,530/300	1,515/98	1,349/53
POOL	1,805/170	1,694/81	1,734/130
GLD	1,427/110	1,543/14	1,434/13
Total:	6,762/665	6,384/267	6,109/309
Molera Reach			
RUN	1,456/295	1,452/116	1,460/48
LGR	1,013/144	1,837/91	1,612/43
POOL	1,180/103	1,483/101	1,398/74
GLD	1,840/101	1,510/24	1,560/10
Total:	5,489/643	6,283/332	6,030/175
Campground Reach			
RUN	1,352/758	1,710/306	1,472/69
LGR	1,059/244	1,785/175	1,651/37
POOL	1,680/1,569	1,840/202	2,127/175
GLD	2,371/281	2,126/90	2,162/5
Total w/o RUN(S)[1]:	6,462/2,852	7,461/773	7,412/286
RUN(S)	755/184	1,797/71	1,729/19
Total w/ RUN(S):	7,217/3,036	9,258/844	9,141/305
Total Area (m^2)/Total Fish:	19,468/4,344	21,925/1,443	21,280/789
Sampling Flows (m^3/s):	0.99-1.44	0.88-1.76	0.65-0.74
Monthly Exceedance (%):	50-65	5-24	9-15

[1] RUN(S) are a mesohabitat type observed in the Campground Reach described as shallow runs with swiftly flowing water, little surface agitation, and no major flow obstructions.

Habitat Availability

Habitat availability data were also equally allocated among reaches and seasons. A total of 1,452 habitat availability samples were collected with 414, 522, and 516 samples collected in the spring, summer, and fall sample seasons, respectively (Table 3). Sample sizes were also generally consistent among reaches. Habitat availability statistics represent the availability measurements made at the same mesohabitat sites where the fish surveys were conducted. The 1D transect data, collected from the 118 transects as outlined earlier, were collected at comparable flows (i.e., 0.68–0.85 m3/s) to the flows (0.65–0.74 m3/s) that existed when the fall fish survey and associated habitat availability data were collected (Table 3).

Table 3.—Statistics for water depth and water velocity habitat availability measurements from the Big Sur River, Monterey County, California during spring 2012, summer 2010, and fall 2010 fish observation sampling events and from measurements at 118 stratified random transects used for a 1D hydraulic habitat model from fall 2011.

Season	Statistic	N	Minimum	Maximum	Average	Median	*SD*
Spring	Water Depth (m)	414	0.02	1.16	0.33	0.30	0.20
	Water Velocity (cm/s)	411	0	190.2	35.7	32.3	27.4
Summer	Water Depth (m)	522	0.02	1.22	0.34	0.30	0.20
	Water Velocity (cm/s)	522	0	172.8	41.8	38.4	28
Fall	Water Depth (m)	516	0.03	1.22	0.28	0.24	0.18
	Water Velocity (cm/s)	516	0	131.7	28	24.7	21
1D (Fall)	Water Depth (m)	4,273	0.02	1.07	0.26	0.24	0.15
	Water Velocity (cm/s)	4,273	0	135.6	27.7	23.8	22

Generally, minimum and maximum water depth habitat availability data were comparable during the spring, summer, and fall sample events (Table 3). Maximum water velocity, on the other hand, showed a general decrease from spring through summer and fall. Similarly, water depth and water velocity were less in fall when compared to the spring and summer sample events. Because the 1D availability data represent a much larger data set (N = 4,273) compared to the availability data from the fall fish surveys (N = 516), these data allow greater insight into habitat availability conditions at the flows when the fall fish surveys were conducted. Comparing the 1D habitat availability data to the fall fish survey habitat availability data indicates the same general occurrence of habitat availability conditions and further indicates a decrease in availability of the higher velocities in fall when compared to summer, and the rarity of depths greater than 1.07 m.

Seasonal Fish Observations

Sample sizes of fish frequencies for spring, summer, and fall sampling events were 4,344, 1,443, and 789, respectively. Most steelhead trout were observed feeding, as opposed to holding.

Steelhead trout <6 cm – spring habitat use.—Steelhead trout <6 cm were found in all habitat types, with approximately 70% occurring in pool and run mesohabitat types in spring. Over 75 percent of the <6 cm fish observed in spring were smaller individuals, 2–3 cm in length, which were observed in locations with water depths ranging from 0.02 to 1.16 m, with a mean of 0.24 m (Table 4).

Table 4.—Habitat use statistics for juvenile steelhead trout observed in the Big Sur River, Monterey County, California in spring 2012, summer 2010, and fall 2010.

Season, size	Statistic	*N*	Minimum	Maximum	Average	Median	*SD*
Spring <6 cm	Water Depth (m)	3,921	0.02	1.16	0.24	0.18	0.17
	Water Velocity (cm/s)	3,920	0	107	15	9.8	14.6
	Fish Focal Point Height	3,921	0	10	6.92	8.00	2.32
	Fish Focal Point Water Velocity (cm/s)	3,905	0	81.4	11.3	7.9	11
	Distance to Escape Cover (m)	3,767	0	3.05	0.44	0.30	0.47
	Distance to Bank (m)	3,921	0	10.0	2.18	1.37	2.0
Summer 6-9 cm	Water Depth (m)	748	.09	1.45	0.41	0.37	0.17
	Water Velocity (cm/s)	748	0	131.4	43.6	42.4	19.8
	Fish Focal Point Height	748	6	10	8.91	9.00	0.82
	Fish Focal Point Water Velocity (cm/s)	740	0	99.1	27.1	25.3	16.8
	Distance to Escape Cover (m)	650	0	3.05	0.92	0.76	0.70
	Distance to Bank (m)	738	0.30	8.84	3.3	3.05	1.50
Fall 6-9 cm	Water Depth (m)	166	0.14	1.31	0.52	0.47	0.26
	Water Velocity (cm/s)	166	0.91	83.5	35.1	34.4	17.4
	Fish Focal Point Height	166	6	10	9.04	9.00	0.84
	Fish Focal Point Water Velocity (cm/s)	166	0	73.8	21.6	21.0	14.3
	Distance to Escape Cover (m)	146	0	3.05	1.17	1.07	0.88
	Distance to Bank (m)	166	0.30	7.32	2.70	2.44	1.44
Summer 10-15 cm	Water Depth (m)	609	0.18	1.45	0.49	0.46	0.19
	Water Velocity (cm/s)	609	1.83	159.7	44.8	43.6	22.3
	Fish Focal Point Height	609	6	10	8.50	9.00	0.82
	Fish Focal Point Water Velocity (cm/s)	605	0	114.3	31.1	29.6	18
	Distance to Escape Cover (m)	523	0	3.05	0.94	0.76	0.69
	Distance to Bank (m)	608	0.30	8.53	3.14	3.05	1.34
Fall 10-15 cm	Water Depth (m)	570	0.17	1.49	0.55	0.52	0.24
	Water Velocity (cm/s)	570	0	136.4	38.7	34.7	24.7
	Fish Focal Point Height	570	6	10	8.74	9.00	0.84
	Fish Focal Point Water Velocity (cm/s)	570	0	102.1	24.4	19.8	17.4
	Distance to Escape Cover (m)	500	0	3.05	1.02	0.91	0.87
	Distance to Bank (m)	570	0.15	7.32	2.60	2.44	1.23

Steelhead trout <6 cm were observed in locations with mean water velocities ranging from 0.0 to 107 cm/s, with a mean of 15 cm/s (Table 4). The focal position of steelhead <6 cm ranged throughout the water column from 0 (surface) to 10 (bottom), but the median fish focal position was 8. Water velocities at the fish focal position ranged from 0.0-81 cm/s with a mean of 11 cm/s.

Greater than 95% of <6 cm steelhead trout were observed at locations near (0.15–0.30 m) some type of escape cover either in form of vegetative or hard substrate types, with hard substrate types (large gravel to large cobble sizes) as the most common (>65%) types. Although <6 cm steelhead trout were observed at locations near escape cover, over 95% occurred at locations with no direct overhead cover. In addition, most <6 cm steelhead were observed within 1.5 m of the bank.

Steelhead trout 6–9 cm – summer habitat use.—Steelhead trout 6-9 cm were found in all habitat types, with most (>65%) occurring in run and riffle mesohabitat types in summer. Steelhead trout 6-9 cm were observed in locations with water depths ranging from 0.09 to 1.45 m, and a mean water depth of 0.41 m (Table 4). Steelhead trout 6–9 cm were observed in locations with water velocities ranging from 0.0 to 131 cm/s, and a mean water velocity of 44 cm/s. The focal position of steelhead trout 6–9 cm ranged from 6 to 10, with a median near-bottom position of 9. Water velocities at the fish focal position ranged from 0.0-99 cm/s.

Steelhead trout 6–9 cm were observed in proximity to a variety of escape cover types, with the most common types being cobble and boulders (65%), followed by branches in water (10%). Although most steelhead trout 6–9 cm were observed to be within approximately 0.6 m of escape cover, only about 13% were observed selecting habitat locations not near (>3 m) any type of escape cover. Further, 99% of all steelhead trout 6–9 cm observations in summer occurred at locations with no overhead cover. In addition, steelhead trout 6–9 cm were observed at a mean distance of 3 m from the bank.

Steelhead trout 6–9 cm – fall habitat use.—Steelhead trout 6–9 cm were found in all habitat types in fall, with most (73%) occurring in pool and run mesohabitat types. Juvenile steelhead trout 6–9 cm were observed in locations with water depths ranging from 0.14 to 1.30 m, and a mean of 0.52 m (Table 4). Steelhead trout were observed in locations with water velocities ranging from 0.91 to 84 cm/s, and a mean of 35 cm/s. The focal position of steelhead trout 6–9 cm ranged from 6 to 10, and a median of 9 (near-bottom). Water velocities at the fish focal position ranged from 0.0 to 104 cm/s.

Steelhead trout 6–9 cm were observed in proximity to a variety of escape cover types in the fall. The most common types of escape cover near the fish observation locations were branches and/or small vegetation (both in-water and out-of-water; 37%) and boulders (13%). Although distance to escape cover ranged from 0 to 3 m, most juvenile steelhead trout were observed to be within approximately 0.9 m of escape cover. Further, over 95% of all steelhead trout 6–9 cm observations in fall occurred at locations with no overhead cover. In addition, steelhead trout 6–9 cm were observed from about 0.30 to 7.3 m from the bank.

Steelhead trout 10–15 cm – summer habitat use.—Steelhead trout 10–15 cm were fairly evenly distributed among run (35%), low gradient riffle (26%), and pool (30%) habitat in summer. Only 9% percent of juvenile steelhead trout 10–15 cm were observed in glide habitat in summer. Juvenile steelhead trout 10–15 cm were observed in locations with water depths ranging from 0.18 to 1.45 m, and a mean of 0.49 m (Table 4). Steelhead trout 10–15 cm were observed in locations with water velocities ranging from 1.8 to 160 cm/s, and a mean of 45 cm/s. The focal position at which the fish were observed ranged from 6 to 10, and had a median of 9 (near-bottom). Water velocities at the fish focal position ranged from 0.0 to 114 cm/s.

Steelhead trout 10–15 cm were observed in proximity to a variety of escape cover types during summer, with the most common being cobble and boulders (54%), followed by branches in water (12%). Most juvenile steelhead trout were observed to be within approximately 0.6 m of escape cover, with a mean distance to escape cover of 0.9 m (Table 4). Further, 99% of all steelhead trout 10–15 cm observations in summer occurred at locations with no overhead cover. In addition, steelhead trout 10–15 cm were observed at distances ranging from 0.3 to 8.5 m from the bank in the summer.

Steelhead trout 10-15 cm – fall habitat use.—Steelhead trout 10–15 cm were found in all habitat types in fall, with most (77%) occurring in pool and run mesohabitat types. Steelhead trout 10–15 cm were observed in locations with water depths ranging from 0.17 to 1.49 m, and a mean of 0.55 m (Table 4). Steelhead trout 10–15 cm were observed in locations with water velocities ranging from 0.0 to 136 cm/s, and a mean of 39 cm/s. The focal position at which the fish were observed ranged from 6 to 10, and had a median of 9 (near bottom). Water velocities at the fish focal position ranged from 0.0 to 102 cm/s.

Steelhead trout 10–15 cm were observed in proximity to a variety of escape cover types in fall. The most common types of escape cover near the fish observation locations were branches and/or small vegetation (both in-water and out-of-water; 44%) and boulders (16%). Although distance to escape cover ranged from 0 to 3 m, most fish were observed to be within approximately 0.0–0.9 m of escape cover (Table 4). Further, over 95% of all steelhead trout 10–15 cm observations in fall occurred at locations with no overhead cover. In addition, steelhead trout 10–15 cm were observed at a range of 0.15–7.3 m from the bank.

Habitat Selection vs Habitat Availability

Water depth (<6 cm steelhead trout).—Depth selection was highly significant (Table 5), since the mean water depth at which steelhead trout <6 cm were found (0.24 m) was significantly shallower than the mean water depth of available habitat (0.33 m). The mesohabitat effect was highly significant (Table 5), with depth use greater in pools and glides than in runs or riffles. Also, there was no significant interaction between depth selection and mesohabitat (Table 5), indicating that differences between habitat used by steelhead <6 cm and available habitat were consistent among mesohabitats.

Water velocity (<6 cm steelhead trout).—There was a highly significant interaction between velocity selection and mesohabitat (Table 5), as steelhead <6 cm generally selected slower moving water (mean 15.0 cm/s) than was available (mean 35.7 cm/s), especially in runs and riffles.

Water depth (6-9 cm steelhead trout).—There was a significant interaction between depth selection, sample period, and mesohabitat type for steelhead 6-9 cm (Table 5). In the run mesohabitat, steelhead 6-9 cm increased their selectivity for deeper water over time. In the riffle and pool mesohabitats, steelhead trout 6–9 cm were found in the deeper water (mean 0.52 m) relative to what was available particularly in the fall (mean 0.28 m) and, to a lesser extent, in summer (mean use and available depths 0.41 m and 0.34 m, respectively; Tables 3 and 4).

Water velocity (6–9 cm steelhead trout).—The interaction between velocity selection, sample period, and mesohabitat type was not significant for steelhead trout 6–9 cm, nor was the interaction between sample period and mesohabitat type (Table 5), indicating that the differences in the availability of water velocity among mesohabitats remained consistent among sample periods. The interaction between velocity selection and mesohabitat type was also not significant (Table 5), indicating that selectivity for water velocity was consistent among mesohabitats. However, the interaction between velocity selection and sample period

Table 5.—Results of two-way and three-way ANOVA for testing effects of water depth and water velocity selection, mesohabitat, and sample period for juvenile steelhead trout in the Big Sur River, Monterey County, California. Significant effects are in bold italics. If interactions are significant, however, ignore the single effects within the interaction, which have been lined out (e.g., ~~0.032)~~ in the table.

Size (cm)	Variable	Factor	df	*F*	*P*
<6	Water Depth	Selection	1, 2266	145.978	***<0.001***
		Mesohabitat	3, 2266	101.889	***<0.001***
		Selection*Mesohabitat	3, 2266	0.950	0.416
<6	Water Velocity	Selection	1, 2265	475.533	~~<0.001~~
		Mesohabitat	3, 2265	30.600	~~<0.001~~
		Selection*Mesohabitat	3, 2265	27.521	***<0.001***
6-9	Water Depth	Selection	1, 2340	65.560	~~<0.001~~
		Sample Period	2, 2340	4.898	~~0.008~~
		Mesohabitat	3, 2340	242.718	~~<0.001~~
		Selection*Sample Period	2, 2340	8.246	~~0.051~~
		Selection*Mesohabitat	3, 2340	2.392	~~<0.001~~
		Sample Period*Mesohabitat	6, 2340	2.332	~~0.026~~
		Selection*Sample Period*Mesohabitat	6, 2340	65.560	***0.030***
6-9	Water Velocity	Selection	1, 2340	3.501	~~0.061~~
		Sample Period	2, 2340	17.404	~~<0.001~~
		Mesohabitat	3, 2340	75.812	***<0.001***
		Selection*Sample Period	2, 2340	4.999	***0.007***
		Selection*Mesohabitat	3, 2340	2.477	0.060
		Sample Period*Mesohabitat	6, 2340	1.173	0.318
		Selection*Sample Period*Mesohabitat	6, 2340	0.700	0.650
10-15	Water Depth	Selection	1, 1920	305.050	~~<0.001~~
		Sample Period	2, 1920	9.563	~~0.002~~
		Mesohabitat	3, 1920	254.211	~~<0.001~~
		Selection*Sample Period	2, 1920	10.220	***0.001***
		Selection*Mesohabitat	3, 1920	8.980	***<0.001***
		Sample Period*Mesohabitat	6, 1920	4.008	***0.007***
		Selection*Sample Period*Mesohabitat	6, 1920	0.808	0.489
10-15	Water Velocity	Selection	1, 1920	40.795	~~<0.001~~
		Sample Period	2, 1920	49.118	~~<0.001~~
		Mesohabitat	3, 1920	98.523	~~<0.001~~
		Selection*Sample Period	2, 1920	13.252	~~<0.001~~
		Selection*Mesohabitat	3, 1920	0.305	~~0.822~~
		Sample Period*Mesohabitat	6, 1920	1.248	~~0.291~~
		Selection*Sample Period*Mesohabitat	6, 1920	3.836	***0.009***

was highly significant indicating that selectivity for water velocity differed among sample periods. Steelhead trout 6–9 cm showed no selectivity in summer (mean 43.6 cm/s), and selectivity for faster water (mean 35.1 cm/s) than what was available in fall (mean velocity available 41.8 cm/s and 28 cm/s in summer, and fall, respectively; Tables 3 and 4). The mesohabitat effect was also highly significant (Table 5), indicating that available water velocities differed among mesohabitats, generally with the greatest velocities occurring in riffle and run mesohabitats.

Water depth (10–15 cm steelhead trout).—The interaction between depth selection and mesohabitat was highly significant with steelhead trout 10–15 cm selecting deeper water (0.49 m and 0.55 m use in summer and fall, respectively; Table 4) than was available (0.34 m and 0.28 m available in summer and fall, respectively; Table 3), especially in pool mesohabitat (Table 5). Similarly, the interaction between sample period and mesohabitat was highly significant. Water depth in riffle, glide and run mesohabitats was slightly deeper in summer but water depth in pool mesohabitat was consistent between sample periods. The interaction between depth selection and sample period was also highly significant indicating steelhead trout 10–15 cm generally selected deeper water than was available, but the difference was most pronounced in fall (mean of 0.55 m and 0.28 m use and available, respectively; Tables 3 and 4).

Water velocity (10–15 cm steelhead trout).—The interaction between water velocity selection, sample period, and mesohabitat was highly significant for steelhead trout 10–15 cm (Table 5). In summer, there was a slight selection for faster water in run, pool and glide mesohabitats, and in fall there was a stronger selection for faster water than was available in all mesohabitat types.

Habitat Suitability Criteria

The equal-area selectivity HSC were developed from the fish frequency data for water depth and water velocity (Figure 2A-J). HSC were developed for steelhead trout <6 cm from the spring sampling event only. In contrast, seasonal umbrella HSC were developed for steelhead trout (6–9 cm and 10–15 cm) for water depth and water velocity to encompass selectivity in both summer and fall rearing periods (Figure 3A and B; Figure 3D and E). Depth HSC remained as separate curves for each size group because of the difference in avoidance of shallow depths between the two size groups (Figure 3C). However, the 10–15 cm velocity curve encompassed the 6–9 cm curve and is representative of both size classes (Figure 3F).

The following selectivity HSC account for (1) differences in fish size; (2) sampling period effects by using spring data for fry, and summer vs. fall umbrella curves for larger juveniles; and (3) for mesohabitat and habitat availability effects through the use of the equal-area sampling approach. All HSC curve points for each size group of juvenile steelhead trout for water depth, water velocity, focal velocity, and distance to escape cover are available in Holmes et al. 2014.

Water depth.—Juvenile steelhead trout avoided shallow water and progressively used deeper water with increasing size. HSC for steelhead trout <6 cm indicate no use of water <0.02 m deep (Figure 2A). Water depth is most suitable (i.e., an index of 1.00) for <6 cm steelhead trout at 0.14–0.16 m. The umbrella HSC for 6–9 cm steelhead trout indicate no use of water <0.10 m (Figure 3A and Figure 3C). Further, water depth is most suitable for 6–9 cm steelhead trout at 0.36–0.46 m during the summer and fall rearing period. The umbrella HSC for 10–15 cm steelhead trout indicate no use of water <0.18 m (Figure 3B and Figure 3C). Finally, water depth is most suitable for 10–15 cm steelhead trout at 0.44-0.51 m during the summer and fall rearing period.

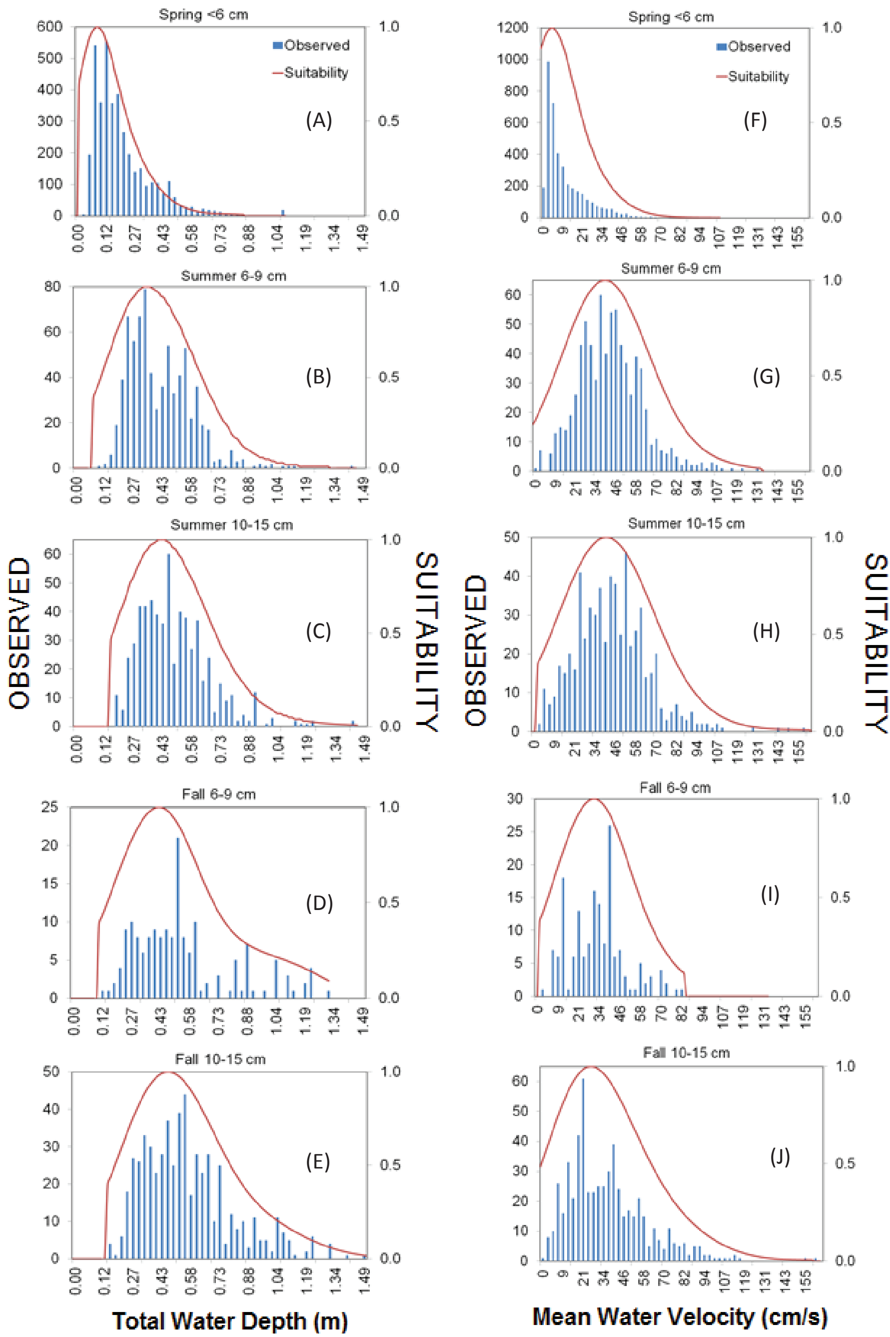

Figure 2.—Total water depths and mean water velocities at focal positions selected by juvenile steelhead trout (bars) according to season and size of juvenile steelhead trout. The solid line is the normalized-kernel smoothed suitability of total water depth and mean water velocity.

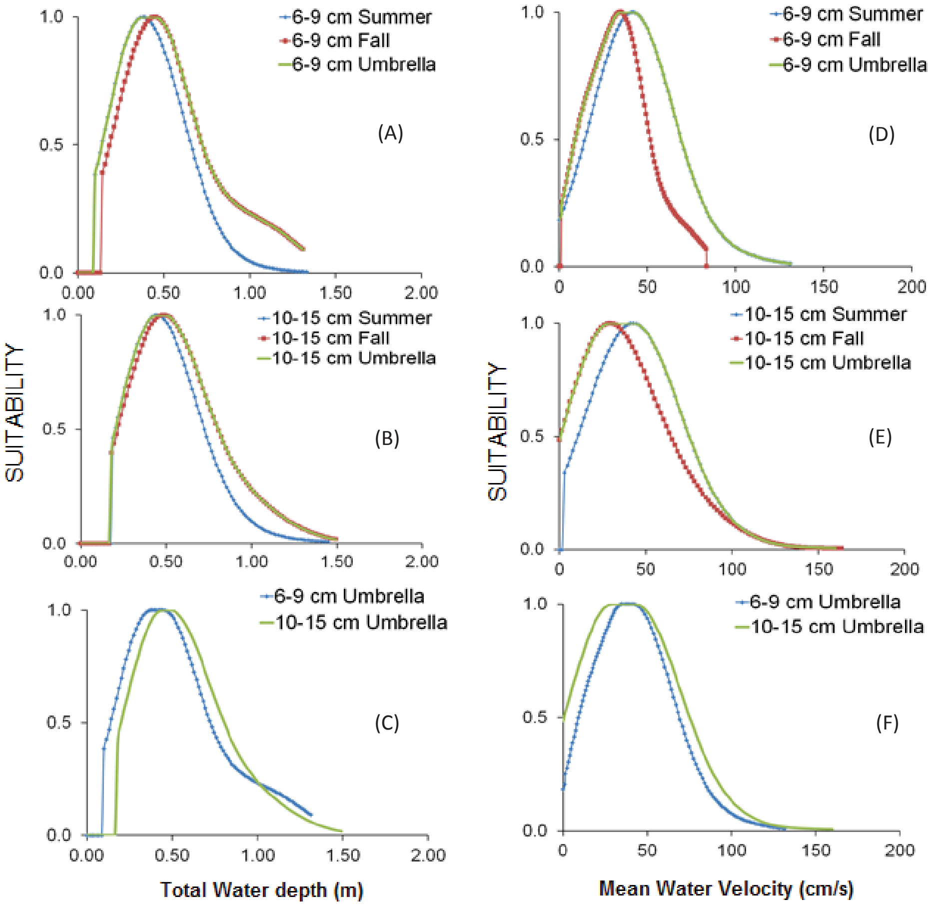

Figure 3.—Comparison of seasonal total water depth and mean water velocity habitat suitability criteria for 6–9 cm and 10–15 cm steelhead trout in the Big Sur River, Monterey County, California. Umbrella habitat suitability criteria curves reflect seasonal use patterns for each size group of juvenile steelhead trout.

Water velocity.—Suitability for water velocity is 1.00 from 5.5 to 7.6 cm/s for steelhead trout <6 cm (Figure 2F). The umbrella HSC for 6–15 cm steelhead trout indicate suitability for water velocity is 1.00 from 27.7 to 44.8 cm/s during the summer and fall rearing period (Figure 3D and Figure 3F).

Fish focal velocity.—Fish focal water velocity HSC for steelhead trout <6 cm is 1.00 from 4.9 to 6.4 cm/s. Fish focal water velocity HSC for 6–9 cm steelhead trout is 1.00 from 22 to 24.7 cm/s. Fish focal water velocity HSC for 10–15 cm steelhead trout is 1.00 from 26 to 29.6 cm/s.

Distance to escape cover.—Distance-to-escape-cover HSC for steelhead trout <6 cm have a 1.00 suitability from 0.24 to 0.27 m. Steelhead trout 6–9 cm distance to escape cover HSC is 1.00 suitability in summer and fall from 0.46 to 0.55 m and 0.58 to 0.73 m, respectively. Steelhead trout 10–15 cm distance to escape cover HSC is 1.00 from 0.55 to 0.64 m and 0.12 to 0.21 m in summer and fall, respectively.

Escape cover types.—In general, hard substrate types (large gravel to large cobble sizes) were the most common types of escape cover observed near the fish observation locations and had the highest HSC. Steelhead trout <6 cm escape cover HSC are 1.00 for small cobble. Steelhead trout 6–9 cm escape cover HSC are highest for large cobble in the summer, and highest for small branches or in-water vegetation <10 cm in the fall. Steelhead trout 10–15 cm escape cover HSC are 1.00 for small boulders in the summer, and highest for small branches or in water vegetation <10 cm in the fall.

Selectivity vs Preference (U/A) HSC Curves

To further evaluate the representativeness of the equal-area selectivity HSC curves, and the potential effects of habitat availability on these curves, alternative HSC curves were derived using the U/A forage ratio methodology (Figure 4, A–J). The smoothed habitat availability curves for depth and velocity were deeper and faster than the fish selectivity curves for steelhead trout <6 cm (Figure 4A and Figure 4F), and resulted in shifts of the preference curves to the left into shallower and slower water. In contrast, the smoothed habitat availability curves were shallower and slower than the fish selectivity curves for steelhead 6–9 cm and 10–15 cm, and frequently resulted in radical shifts of the preference curves to the right (Figures 4B and Figure 4C, and Figure 4G and Figure 4H, respectively). These shifts for steelhead trout 6–9 cm and 10–15 cm were particularly extreme for the fall data, and resulted in high suitability for depths greater than 1.2–1.5 m and velocities greater than 107 cm/s while severely deflating the suitabilities where the majority of fish were observed (Figure 4D and Figure 4E, and Figure 4I and Figure 4J, respectively). Trimming or truncating (or both) the U/A data was (were) unsuccessful at producing preference curves that were not radically shifted to the right for 6–9 cm and 10–15 cm steelhead trout.

Discussion

Steelhead trout life history tactics and thresholds.—Big Sur River steelhead trout were observed selecting faster velocity habitats as the rearing fish grew during the spring and summer seasons, consistent with Everest and Chapman (1972) as well as by more recent observations on the Klamath River (Hardy and Addley 2001, Hardin et al. 2005). Interestingly, the fastest velocities selected by all steelhead (fry and larger juveniles) on the Big Sur River were observed to occur in the summer, not the fall rearing period. These findings are consistent with Allen (2000), who found that juvenile spring-run Chinook salmon (*O. tshawytscha*) selected faster velocities in summer over fall in the Yakima River, Washington. There was also good overlap of the Big Sur River HSC velocity curves for both larger size groups of steelhead trout, and the resultant velocity umbrella curve was comparable in peak and overall shape with historical steelhead HSC (Bovee 1978).

The 10–15 cm steelhead trout showed a slightly increased selectivity for faster velocities greater than 61–91 cm/s over the 6–9 cm steelhead trout in the summer, while also showing higher selectivity for slower velocities than the 6–9 cm fish in the fall. These results are generally consistent with Spina (2003), who reported that larger juvenile steelhead trout, ages 1 and 2, selected slower water velocity habitats than young-of-year in Santa Rosa Creek, approximately 129 km south of the Big Sur River. As flows receded in the Big Sur River during fall, larger juvenile steelhead trout showed higher selectivity for deeper, slower

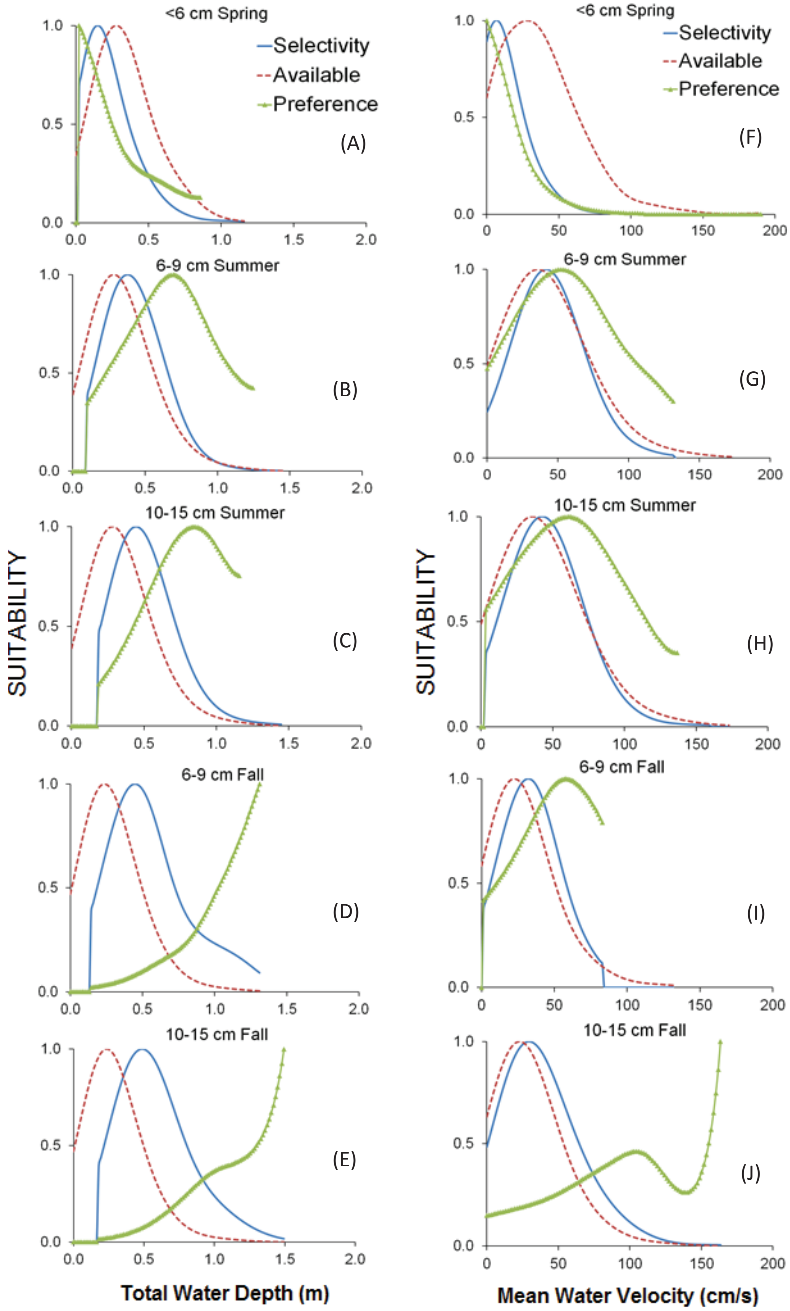

Figure 4.—Comparison between juvenile steelhead trout (according to size) selectivity habitat suitability criteria using equal-area sampling with habitat availability and preference habitat suitability criteria using forage ratio mathematical adjustments; Big Sur River, Monterey County, California.

water velocity habitats that occur in pools. The smaller, 6–9 cm young-of-year steelhead trout, on the other hand, selected faster velocity habitats despite the rare occurrence of such habitat in the fall compared to summer. Increased use of pools and deeper habitats by the larger juveniles in the fall may be related to other non-hydraulic habitat factors such as bioenergetics, predation, or temperature.

Steelhead trout temperature tolerance varies among life stages (Bell 1986, Bjornn and Reiser 1991), and differences in seasonal water temperatures may affect habitat selection (Reeves et al. 2009). The drop in mean temperatures from 16° C in summer to 14° C in fall could be associated with increased use of deeper and slower pool habitats. A similar change in water temperatures may have influenced a shift in microhabitats selected by juvenile spring-run Chinook salmon in the Yakima River, Washington (Allen 2000). However, these temperatures are well above the 5–10° C temperatures known to elicit significant shifts in behavior in steelhead and rainbow trout in colder, interior climates (Chapman and Bjornn 1969, Bustard and Narver 1975, Riehle and Griffith 1993).

Hardy and Addley (2001) also observed juvenile steelhead trout selecting deeper water habitats in fall versus spring on the Klamath River. Thus, it is apparent that steelhead trout select deeper water (and faster velocity) habitats as they grow. However, the depth thresholds (minimum depth avoidance) observed by the rearing (non-fry) steelhead trout in the Big Sur River have not been found by other researchers (Waite and Barnhart 1992; Hardy and Addley 2001) or to be as distinct between juvenile size groups in studies on other coastal California rivers. On the Big Sur River, 95% of all juvenile steelhead ≥6 cm FL ($N = 2{,}093$) avoided water depths shallower than 0.23 m during the core rearing period of summer and fall.

In addition to hydraulic microhabitat conditions (i.e., water depth and velocity), rearing site selection of Big Sur River steelhead trout was influenced by factors such as proximity and type of in-water escape cover. Despite some juvenile steelhead trout not being observed near (i.e., <3 m) any type of escape cover, all size groups of juveniles were predominately observed in close proximity to some type of in-water escape cover, with types ranging from gravel/cobble for <6 cm steelhead trout to larger cobble and small boulders for larger juvenile steelhead trout. Although proximity and type of escape cover shifted with fish size, it also shifted with season and associated flow conditions (Holmes et al. 2014).

We observed juvenile steelhead trout shifting selection of rearing sites in close proximity to hard substrate escape cover types (i.e., cobble and boulder) in summer to selection of rearing sites in close proximity to predominately vegetative escape cover components (i.e., branches <10 cm diameter in-water) in the fall. This seasonal shift was apparently not directly due to respective availability of sites in proximity to those escape cover types between summer and fall. Instead, we attributed this shift to decreased availability of faster water velocities in the fall or the faster areas becoming too shallow, or both. For example, juvenile steelhead trout were observed selecting feeding locations in the summer with faster water velocities near hard substrates, which may act as both in-water escape cover and water velocity shelter. In the fall, however, flow levels decline naturally on coastal California streams and rivers and the corresponding water velocities also slow making such faster velocity habitats rare or too shallow for larger juveniles.

Hardy and Addley (2001) also observed seasonal shifts in proximity of steelhead trout to hard substrates (i.e., small boulders) and vegetative-type (e.g., shrubs, grass, sedges, herbs) escape cover on the Klamath River. However, the trend they observed was opposite of what we observed on the Big Sur River. The opposing trends are likely related to the fact that Klamath River vegetative cover was only available under high spring flows as well as differences in the physical channel and riparian habitat between the much larger Klamath River Basin (i.e., 40,790 km^2) and the smaller redwood-dominated Big Sur River Watershed (i.e., 160 km^2). Waite and Barnhart (1992) cautioned applying HSC from one river system to another without consideration of site-specific hydrology and habitat characteristics.

Equal-area sampling vs. forage ratio adjustments.—Flow conditions during the fish surveys, with the exception of the fall sampling event, occurred at annual exceedance probability flows below the Big Sur River's 50% annual exceedance probability benchmark. However, comparison of timing of fish surveys with monthly exceedance probability flows indicates summer and fall sampling occurred at above average flows ranging from 5 to 24% exceedance probability. We conclude habitat availability was good to optimal based upon site-specific water availability since the sampling flows during the core rearing period of summer and fall were comparable to those of above average or wet months (Table 2). A central tenet of developing HSC is that all micro- and macrohabitats should be equally available for the organism to select from (Bovee 1986). Since stream flow is associated with juvenile steelhead survival (Grantham et al. 2012) and to salmonid habitat use (Ptolemy 2013), sampling for HSC development at lower than average natural flows may not provide equal availability of all habitats and may limit the effectiveness of an equal-area sampling approach. In such cases, corrective methods to adjust for habitat availability, such as application of the forage ratio, may be necessary.

Big Sur River steelhead trout HSC, which far exceeded minimum sample size requirements as outlined by Bovee (1986), were developed using habitat utilization data that were not mathematically adjusted for habitat availability. Instead, we employed a rigorous effort to maintain equal-area sampling among mesohabitat types, river reaches, and sampling seasons. Equal-area sampling within mesohabitat types helps minimize biases by allowing relative quality of the different habitat types to dictate the form of the HSC (Allen 2000). Further, use of the equal-area sampling design under natural unimpaired flow conditions accounts for potential biases of flow-related habitat availability (i.e., avoids confusing selection or use of optimal habitat with selection or use of merely tolerable habitat) on development of site-specific HSC. Our study design using equal-area sampling allowed the species and its respective life stages to inform us of its biological habitat requirements, without the need for mathematical adjustments (i.e., forage ratio adjustments) of habitat use with habitat availability data.

Using the equal-area selectivity HSC approach avoids potential pitfalls associated with development of preference HSC other researchers have identified (Bovee and Zuboy 1988, Hayes and Jowett 1994, Payne and Allen 2009). For example, small sample sizes, particularly at the tails or extremes of the frequency distributions of habitat parameters, can result in potential overcorrection for habitat availability when using the forage ratio adjustments, as seen with the Big Sur River depth and velocity HSC. Our observations (Figure 4) were, therefore, consistent with those of Hayes and Jowett (1994), which indicate performing the forage ratio adjustment for habitat availability when populations are not limited by habitat or when sampling bias is not suspected (Payne and Allen 2009) may result in over-corrected HSC (Bovee et al. 1998). Other researchers have also justified use of HSC based upon the utilization data without a preference adjustment for habitat availability (Johnson 1980).

We contend that development of preference HSC may well be a viable option for development of HSC in those instances when sampling conditions are known or suspected to be limited by habitat availability, or where inequalities in sampling effort among habitat types leads to biases in the use data. In such cases, selectivity HSC based solely on equal-area sampling may not yield HSC that are unbiased by habitat limitations. Equal area sampling may also be highly inefficient where a species or life stage is largely confined to limited habitat conditions, such as salmonid spawning which is limited to specific locations where appropriate substrate is available, or for obligate pool- or riffle-dwelling species that rarely occupy other habitats.

We observed juvenile steelhead trout habitat selectivity changing with fish size, season, discharge, and habitat availability. Biologically accurate and unbiased HSC are critical for valid and biologically representative hydraulic habitat modeling of flow and habitat relationships. There are many potential pitfalls in developing site-specific HSC that could contribute to defective HSC and hence unreliable instream flow modeling efforts, which include (1) inadequate overall sample sizes; (2) unequal or insufficient representation of habitat use; (3) habitat availability being unaccounted for, which may mask flow-linked constraints on habitat use; (4) limited temporal sampling such as during one timeframe or season of an important life history component of a species (although one timeframe or season may be fine for certain applications such as spring sampling for salmon fry that emigrate soon after emergence); and (5) uncritical application of ratio-based curves that bear little resemblance to the underlying use data. Our sampling strategy and the overall ecologically favorable stream conditions of the Big Sur River minimized the potential bias of sampling techniques and habitat availability. Use of corrective mathematical methods (i.e., using availability data) were evaluated, but were not effective or warranted based upon the enhanced flow conditions observed during sampling and the overall ecologically favorable habitat conditions of the Big Sur River. With proper habitat stratification and non-limiting sampling conditions (e.g., adequate flows and non-degraded habitat), use of an equal-area sampling design for site-specific HSC development is, therefore, a viable option for development of biologically relevant and representative HSC and, ultimately, for effective environmental flow recommendations.

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