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[Management Brief]

Downstream Migration, Rearing Abundance, and Pool Habitat Associations of Juvenile Steelhead in the Lower Main Stem of a South-Central California Stream

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Abstract.—Unlike river main stems in the northern geographic range of steelhead *Oncorhynchus mykiss*, the surface flow of main stems in south-central and southern California can be extremely low, intermittent, or entirely lacking during the dry season. This has led to a general belief among biologists that main stems provide only migratory habitat, which has created challenges for fishery managers because some main stems are now perennial as a result of the continuous release of treated municipal wastewater. During 2000–2002, we monitored juvenile abundance and downstream migration of the south-central California coast evolutionarily significant unit of steelhead in the lower main stem (reaches proximate to the ocean) of a south-central California stream. This stream has a continuous discharge of tertiary-treated municipal wastewater that forms most, if not all, of the dry-season living space for steelhead. Our principal finding indicates that this artificial discharge provides oversummering habitat for juvenile steelhead.

The function of river main stems in the ecology of anadromous salmonids transcends linking spawning and rearing areas with the ocean. Main stems provide areas where juveniles rear before ocean entry (Leider et al. 1986; Loch et al. 1988; Murphy et al. 1997) and where different size- or age-classes of conspecifics can exploit a diversity of habitats (Murphy et al. 1989; Johnson et al. 1994), thereby promoting multiyear freshwater residence (Spina 2003). The seasonal pattern of juvenile migrations into main-stem habitats (Peterson 1982; Tschaplinski and Hartman 1983; Hartman and Brown 1987; Bramblett et al. 2002) suggests these areas possess characteristics that are essential for freshwater survival of anadromous species.

The characteristics of migrant juvenile steelhead *Oncorhynchus mykiss* and their downstream migration are largely unknown in the southern geographic range of this species (Fukushima and Lesh 1998). Life history characteristics may differ from those of their northern counterparts because variations in the life history of anadromous salmonids (Withler 1966) can be attributed, in part, to heterogeneous environmental conditions (Metcalfe and Thorpe 1990; Taylor 1990; Connor et al. 2002) and climatic differences between the species' southern (California) and northern (Alaska) ranges. Knowing their migration characteristics, particularly as they relate to entry into river main stems, would be useful for developing strategies to conserve steelhead populations.

This paper reports the findings of a 3-year study (2000–2002) on the downstream migration and abundance of the south-central California coast evolutionarily significant unit of steelhead in the lower main stem (reaches proximate to the ocean) of a south-central California coastal stream. This stream receives a continuous discharge of tertiary-treated municipal wastewater that provides most, if not all, of the dry-season living space for juvenile steelhead. Our objectives were to (1) assess whether downstream migrations included parr and smolts; (2) document the seasonal timing of the downstream migration and length of the migrants; (3) investigate whether the migration corresponded to environmental factors; (4) estimate the abundance of juvenile steelhead in the lower main stem during summer and early fall (what we believe is the ''nonmigratory'' season for steelhead in this region); and (5) determine relationships between

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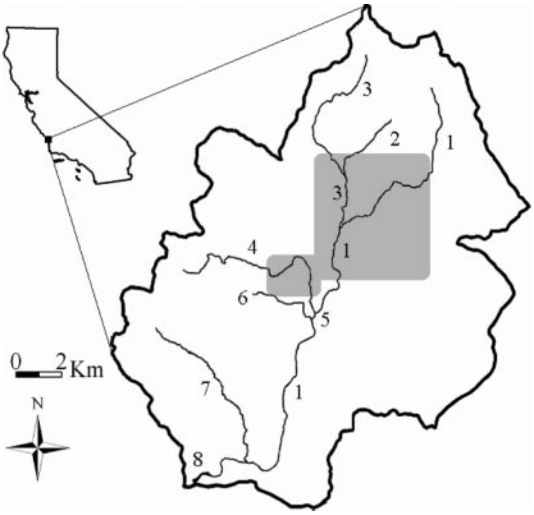

FIGURE 1.—Location of the San Luis Obispo Creek watershed, the wastewater treatment facility, and principal streams (1 = San Luis Obispo Creek, 2 = Brizziolari Creek, 3 = Stenner Creek, 4 = Prefumo Creek, 5 = wastewater treatment facility and point of wastewater release into San Luis Obispo Creek, 6 = Froom Creek, 7 = See Canyon Creek, 8 = estuary). The study area lies between the wastewater treatment facility and the estuary, a distance of 9.7 km. The shaded portion approximates the urban area.

counts of steelhead and pool characteristics in the lower main stem.

Study Area

San Luis Obispo Creek in San Luis Obispo County, California, originates at an elevation of 670 m and flows directly into the Pacific Ocean (Figure 1). Runoff characteristics within the creek's drainage (215 km^2) are similar to those of other unregulated regional streams, which exhibit low discharge except during and shortly after periods of precipitation (U.S. Army Corps of Engineers 1999). Juvenile steelhead have been observed throughout much of San Luis Obispo Creek and its principal tributaries (Brizziolari, Prefumo, Froom, Stenner, and See Canyon creeks), and one of us (A.P.S.) has observed steelhead spawning in the upper reaches of San Luis Obispo Creek and in See Canyon Creek.

Our study was conducted in a 9.7-km reach of San Luis Obispo Creek (Figure 1). The area is generally rural; the bulk of the urbanized area lies in and adjacent to the City of San Luis Obispo, which is upstream of the study reach. Willows *Salix* spp., white alders *Alnus rhombifolia*, and California sycamores *Platanus racemosa* border the creek within the study area. Pools, shallow riffles, and runs are present in the area and some contain accumulations of tree branches. The channel bed consists of mostly gravel and smaller particles. Average wetted width of the creek during summer was 6.3 m. Depth of pools, the sampling unit in our study, averaged 33 cm and pool surface area averaged 143 m^2 over the period of investigation.

At the upstream boundary of the study reach, tertiary-treated municipal wastewater is released into the creek at a relatively constant 0.2 m^3/s and represents most, if not all, of the surface water in the study reach during the dry season. This is because portions of the main stem reaches in the upper watershed and tributaries typically experience intermittent or an absence of surface flows during the dry season. The City of San Luis Obispo's process for treating the wastewater generally involves screening, grit removal, primary clarification, biofiltration, clarification, activated sludge, clarification, effluent cooling (during summer), filtration, disinfection with sodium hypochlorite, and dechlorination with sodium bisulfate. During the treatment process, ionized and un-ionized ammonia is converted to nitrate, though the concentration of nutrients in the wastewater is not lowered. In summer and fall 2000–2002, water temperature ranged from 15°C to 22°C and clarity (distance to a 5-cm-long object) ranged from 1 to 2 m throughout the lower main stem, which was largely because of the released wastewater.

Methods

Characteristics of the migration and the migrants.—An Alaskan A-frame weir that extended the full width of the creek and was adjacent to the water reclamation facility (Figure 1) trapped downstream migrants from mid-March through December 2000–2002. The weir was constructed of paired, horizontal, 2.4-m aluminum channeling that had 2.5-cm-diameter perforations for holding 50 pieces of 1.2-m-long × 2.5-cm-diameter plastic conduit vertically. Plastic netting (1.2-cm mesh) was placed along the lower half of the weir panels. The weir directed fish into a 20-cm-diameter × 6-m-long plastic pipe that was attached to a submersed fish-holding box. Although study objectives did not include estimating the number of migrants, we wanted an understanding of how well the trap functioned. Each year at the beginning of the trapping season, a known number of marked (with ink) fish were released 30 m upstream of the trap at a variety of discharges to assess trapping efficiency (typically no less than six individuals

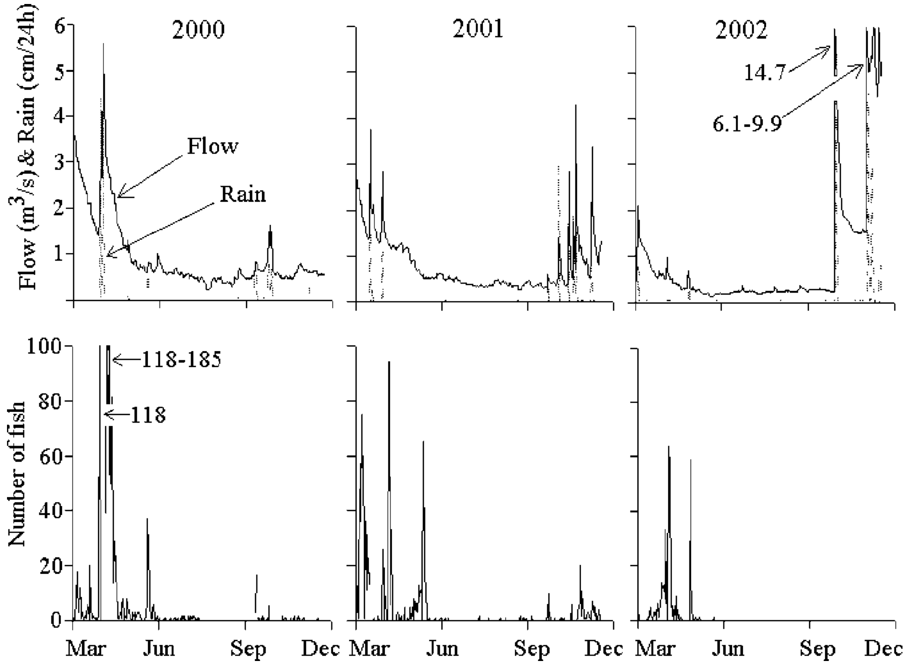

FIGURE 2.—Precipitation (vertical stippling), estimated discharge, and number of juvenile steelhead captured in a downstream migrant trap at San Luis Obispo Creek from March through December 2000–2002. Dates when the trap was inoperable were 17–18 April, 12 July, and 29 October–3 November 2000; 7 April, 18 June, 9 August, and 13, 25, and 29 November–3 December 2001; 25 March, 12 July, 8–10 and 19 November, and 17 December 2002. Tick marks along the *x*-axis represent the middle of the indicated month.

for each of at least three trials performed on a minimum of two dates). San Luis Obispo Creek is a small, shallow stream; we believe the numbers of fish used to assess trap efficiency were reasonable. Recaptures of marked individuals ranged from 38% to 55%, but peak flows during one of our efficiency assessments rendered the trap inoperable. There were only a few occasions each year when exceptionally large winter flows (or vandals) affected trap operation (see Figure 2 for dates the trap was inoperable). Our trapping efficiency was within the range reported by other investigators who, in fact, have enumerated abundance of anadromous salmonids (Ward and Slaney 1988; Thedinga et al. 1991; Murphy et al. 1997; Roper and Scarnecchia 1999). During the trapping season, the trap was frequently inspected for fish each morning.

All steelhead were measured to the nearest millimeter (fork length [FL]) and examined for evidence of smolting (absence of parr marks, external silvering, and blackened fin margins [Wedemeyer et al. 1980]; large head, slender body, and long caudal peduncle [Beeman et al. 1995]). Juvenile steelhead that showed characteristics between parr and smolt (e.g., no evidence of parr marks and external silvering or blackened fin margins) were classified presmolts; our classification of parr included age-0 steelhead. The same field personnel typically performed the daily classifications and were given the same set of criteria (including color photographs of parr, presmolts, and smolts), along with instructions on how to interpret external characteristics and classify individual specimens. We recognize that the physiological definition of a smolt can be complex (e.g., review by Hoar 1976), but we chose to use the term ''smolt'' to distinguish one life stage classification from the other two life stage classifications. Only fish up to 300 mm FL were included in the analyses (this size category is similar to the maximum size of smolts reported by other investigators; Leider et al. 1986; Ward and Slaney 1988; Peven et al. 1994). Three larger steelhead measuring 303, 324, and 380 mm FL were captured as well as 17 fish ranging from 400 to 595 mm FL.

We tabulated the dates when parr, presmolts, and smolts were captured in the trap and calculated a median date to characterize migration timing. Polynomial regression was used to model the relationship between daily mean length of trapped fish and time of capture in days. The contribution of the quadratic term (i.e., β_2, the effect parameter for the squared day-of-capture variable) was assessed by means of the extra-sum-of-squares method (Montgomery and Peck 1992). The fit of the model and appropriateness of the parameter estimates were assessed by means of standard methods (Montgomery and Peck 1992; Engelman 1998). The R^2 reported in Results is the correlation between the original observed values and the values predicted by the relationship between daily mean length of trapped fish and time of capture (Engelman 1998). One-way analysis of variance was used to assess the difference in the mean length of parr, presmolts, and smolts among the 3 years of data. Mean fish length was calculated for each day of trapping in which fish within a particular life stage classification were collected (i.e., a single ''trap haul'' was considered an independent sample). Tukey's test was used to determine which mean lengths were different from one another. The type I error rate was 0.05 for all analyses.

Relationships between the characteristics of the downstream migration and environmental factors were assessed based on daily rainfall data (cm/24 h) obtained from the National Weather Service (San Luis Obispo Airport) and discharge information. San Luis Obispo Creek does not have a stream gauge, but measurements ($N = 40$) of discharge were obtained during our study. Therefore, we predicted daily discharge (m^3/s) in San Luis Obispo Creek using a least-squares regression model ($r^2 = 0.93$; $P < 0.0005$; $Y = 0.6X - 0.2$) based on daily mean discharge data from a nearby stream (Lopez Creek [U.S. Geological Survey stream no. 11141280]; drainage area, 54.1 km^2) and the 40 measurements of discharge in San Luis Obispo Creek. The sign and magnitude of the estimated parameters in our regression model were reasonable, and no model deficiency was apparent based on examination of residual plots. To further evaluate the appropriateness of this model for predicting discharge, we used the duplex algorithm as a basis to split the original 40 observations (i.e., paired measurements of discharge in San Luis Obispo and Lopez creeks) into equal ($N = 20$) estimation and prediction data sets (Montgomery and Peck 1992). A least-squares regression model was developed from the estimation data set, and the resulting parameters were used to predict values (based on the prediction data set selected by the algorithm) for comparison with the original observed values (i.e., prediction data set). Differences between observed and predicted values were typically less than 0.3 m^3/s at relatively low to moderate estimated discharges (<4 m^3/s), but observed high discharges were typically overestimated by as much as 2 m^3/s. This suggests high discharges in San Luis Obispo Creek were lower than indicated by our estimates, which probably reflects the fact that most discharge measurements were taken during times of relatively low discharges.

Multiple linear regression analysis was used to assess the contribution of daily estimated discharge and month (treated as a dummy variable) for predicting the daily catch of juvenile steelhead. The month term in our regression model was used to represent seasonal influences, such as temperature and photoperiod (increasing day length reaches a maximum on or about 22 June). Regression diagnostics (Wilkinson and Coward 1998) indicated that the quantitative variables be transformed ($\log_e[X + 1]$ was selected to account for zero and near-zero values; Zar 1996).

Monitoring steelhead abundance.—From 2000 through 2002, we employed a modified Hankin and Reeves (1988) approach for estimating the abundance of juvenile steelhead. The approach involved conducting single-pass dive surveys (using mask and snorkel) in randomly selected habitat units and then calibrating counts obtained from the single-pass surveys in a random subset of habitat units (typically six for each monthly survey) using the method of bounded counts (i.e., three additional dives of the subject unit were performed that provided counts from a total of four dives) (Mohr and Hankin, in press). The approach employs additional dives in a calibration unit when the fish count obtained from the initial single-pass survey of the subject unit is up to 20 individuals. By contrast, when the fish count obtained from the initial single-pass survey is more than 20 individuals, electrofishing (e.g., based on removal-depletion methods) is employed because, in part, the bounded count estimator possesses unacceptable bias and double counts of fish are likely. In an effort to reduce survey costs and minimize harm to steelhead, we conducted additional dives alone even when fish counts from the initial single-pass survey exceeded the 20-fish criterion (of the 50 pools randomly selected for calibration in our study, only 9 of the initial single-pass survey counts exceeded the recommended maximum of 20 fish). Although we did not use electrofishing, counts from the multiple dives still provided a means to calibrate the single-pass dive counts and to develop abundance estimates and related errors for the expanded estimates (in our case, number of fish/km of pools).

We applied this approach during July, August, and September (2000–2002) and October (2002 only) in pools randomly selected from a preexisting habitat map for the study area. In July 2000, 12 pools were surveyed, whereas 25 pools were snorkeled during each subsequent month. Depending on pool width, 1–3 divers entered a pool and moved upstream in unison within predetermined dive lanes, noted the number of juvenile steelhead, and assigned individuals to one of two size-classes ($<$10 cm TL, $\geq$10 cm TL). Divers employed a standard procedure to thoroughly search each sample unit for steelhead. This included moving slowly upstream, frequently pausing to scan the channel bed and water column for fish before progressing further upstream, and inspecting interstitial spaces between and underneath woody debris and rocks. Divers usually allowed 15 min to elapse before repeating a subsequent dive to ensure similar water clarity among counts (i.e., as required for calibration owing to the method of bounded counts). Pool length (m), width (m), and depth (cm) at multiple locations were measured after diving. Count data collected from dives in the calibration pools were used to estimate abundance of steelhead in those pools and to estimate a bias adjustment factor for the diver observation probabilities (Mohr and Hankin, in press). A two-stage ratio estimator was used to estimate the total number of steelhead (according to size-class) in all divable pools in the study area using pool length as an auxiliary variable (Hankin 1984). Multiple-regression analysis was used to test the contributions of depth, surface area, location of the sampled pools, and month to explain variation in counts (obtained from the initial single-pass survey) of juvenile steelhead in the sampled pools within each year (although other habitat variables may have provided additional information concerning pool habitat associations, only depth and surface area were consistently quantified each year). Regression diagnostics followed standard methods (Wilkinson and Coward 1998). A square-root transformation applied to the counts of juvenile steelhead was occasionally necessary to achieve normality and to stabilize error variance. Analyses were performed separately for small ($<$10 cm TL) and large ($\geq$10 cm TL) juvenile steelhead.

For many reasons, our estimates of juvenile steelhead abundance in the lower main stem should be considered only an index of the true abundance. At times, water clarity in our study fell below the minimum recommended for direct underwater observation (Cunjak and Power 1986). We only sampled pools, and although the sampled pools contained woody debris, pools with extensive accumulations of brush were not included in the sampling design because, based on prior experience, we expected snorkeling would have proved ineffective in such habitats. These habitats, for example, represented about 27% of the available habitat (by length) in 2002, whereas the pools we sampled represented 25% of the available habitat. Based on the function and value of woody debris to stream fish populations, excluding pools with extensive brush might have precluded observing a number of fish (review by Bryant 1983; Elliott 1986; Lisle 1986). We did not apply electrofishing as a means to assess true abundance of juvenile steelhead, and diver movements in a sample unit may have caused fish to evade diver detection (Thompson 2003); however, we did at times employ an additional diver (or an observer on the creek bank) near the upstream boundary of the sample unit to note any fish leaving the sample unit. We rarely observed fish leaving a sample unit and believe juvenile steelhead, in response to divers, probably sought shelter within a sample unit because extremely shallow water bounded our sample units (pools) and cover was available. Overall, we believe our application of the Mohr and Hankin (in press) protocol and the resulting index estimates are reasonable for the intent of our study.

Results

Characteristics of the Migrants and Migration

Estimated discharge during trapping was highest in spring and lowest in fall; the exception was in 2002, when precipitation late in the year increased discharge and exceeded the estimated spring discharge (Figure 2). Several spring storms in 2000 and 2001 caused peaks in discharge, while spring precipitation in 2002 was negligible. The total annual rainfall was 53.1 cm in 2000, 47.2 cm in 2001, and 22.4 cm in 2002. The 53-year average annual precipitation for the San Luis Obispo area is 59.9 cm.

Downstream migration of juvenile steelhead occurred from March through May of each year. There was also a small secondary migration in the fall of 2000 and 2001 (Figure 2). Smolts were found in the trap only during the spring of each year (Figure 3). The majority of presmolts were

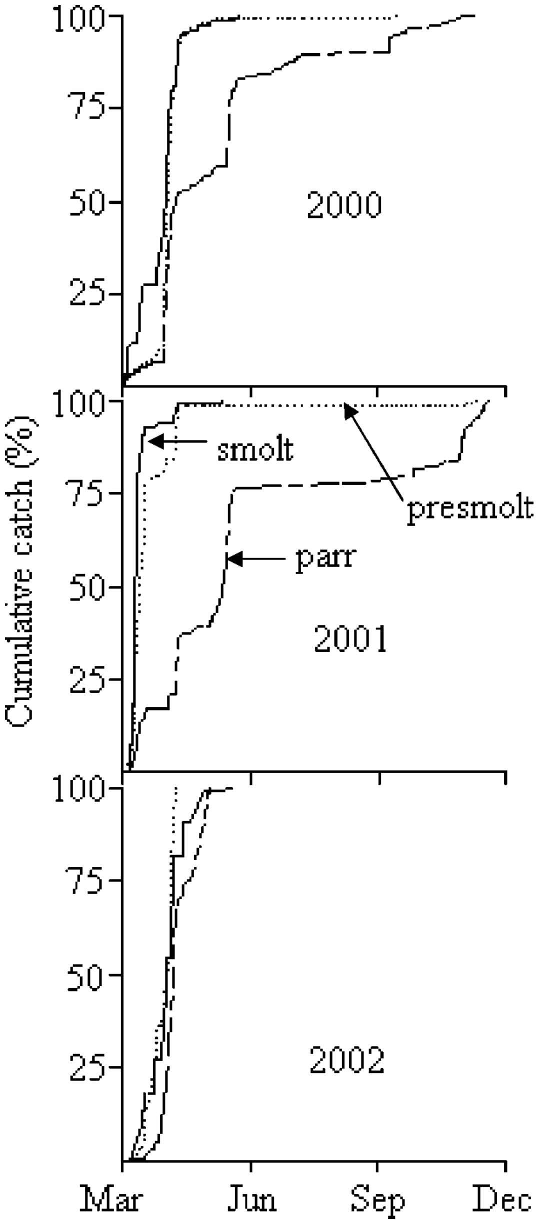

FIGURE 3.—Cumulative catch of parr, presmolts, and smolts in a downstream migrant trap at San Luis Obispo Creek from March through December 2000–2002. Tick marks along the *x*-axis represent the middle of the indicated month.

found in the trap during spring, but a few presmolts were captured during the late fall and early winter of 2000 (4 individuals) and 2001 (10 individuals). Parr were found in the trap throughout most of the trapping season. The maximum peak daily capture of juvenile steelhead decreased among years, but the peak date of capture was consistently in April (Table 1). Smolts generally migrated earlier (based on the median date) than presmolts and parr, and presmolts migrated earlier than parr. No smolt was captured after 1 June of any year. In 2002, the median date of migration was much earlier for parr than in the previous two years. Generally, the percentage of parr in the catch exceeded that of presmolts and smolts, and relatively few smolts were captured throughout the study period.

Migrants, on average, were larger early and late in the trapping season than in the middle (summer) of the season (Figure 4). For each year, the regression model (including the linear and quadratic terms) was significant (all $P < 0.001$); the quadratic term contributed for predicting daily mean fish length (all $P < 0.001$). The R^2 for each annual model ranged from 35% (2002) to 51% (2000). Parr, on average, were smaller than presmolts and smolts, and presmolts were smaller than smolts (Table 1). The mean length of parr differed among years ($F_{2,221} = 12.8$; $P < 0.0005$), and the post-comparison test indicated the mean lengths of parr determined for each year differed from one another (all $P \leq 0.03$). For presmolts, the mean length did not differ among years ($F_{2,98} = 0.3$; $P = 0.8$). Smolt mean length was different among years ($F_{2,41} = 4.3$; $P = 0.02$), and smolts in 2001 were larger than smolts in 2000 ($P = 0.02$) but not different in terms of length from smolts in 2002 ($P = 0.5$). Mean smolt length was similar in 2000 and 2002 ($P = 0.6$).

In regard to relationships with environmental factors, the pattern of downstream migration appeared to correspond with season and with periods of elevated estimated daily discharge (Figure 2). The multiple-regression model indicated that daily discharge ($P < 0.0005$) and month ($P < 0.0005$) predicted the daily catch of juvenile steelhead in 2000. Likewise, for 2001, discharge ($P = 0.02$) and month ($P < 0.0005$) contributed to the model. In 2002, estimated discharge was relatively low and fluctuated little during the trapping season, so it did not contribute to predicting the daily catch of juvenile steelhead ($P = 0.9$), but month did ($P < 0.0005$). Duration of the downstream migration was abbreviated in 2002 relative to that observed the previous two years. Only minor rainfall events occurred after trap installation in late March (Figure 2). Because peak flows seem to be at a time of high migrant movement in San Luis Obispo Creek, we probably missed capturing fish during times when flows were high and the trap was inoperable (e.g., fall of 2002). Therefore, the pro-

TABLE 1.—Characteristics of downstream migrant juvenile steelhead and the downstream migration at San Luis Obispo Creek between March and December 2000, 2001, and 2002. The sample size *N* refers to the number of times the trap captured individuals of each life stage classification and the total number of individuals of the specific life stage (in parenthesis) captured. Abbreviations are as follows: p = parr; ps = presmolt; s = smolt.

Year	Maximum number of steelhead captured; date	Maximum number of smolts captured; date	Date of last smolt	Smolt fork length (mm)	*N*	Mean fork length (mm ± SD)	Percentage of life stage in catch	Median migration date
2000	185; Apr 20	11; Apr 23	Jun 1	130–203	99 (404) p	95 ± 31 p	27 p	Jun 3 p
					58 (1,033) ps	144 ± 23 ps	68 ps	Apr 26 ps
					28 (83) s	157 ± 16 s	5 s	Apr 18 s
2001	94; Apr 29	33; Mar 29	May 27	117–234	90 (557) p	84 ± 33 p	54 p	Jun 17 p
					30 (372) ps	148 ± 28 ps	36 ps	Apr 9 ps
					11 (103) s	177 ± 28 s	10 s	Apr 6 s
2002	64; Apr 26	3; Apr 26	Apr 26	155–213	35 (340) p	65 ± 12 p	88 p	Apr 30 p
					13 (33) ps	142 ± 41 ps	9 ps	Apr 18 ps
					5 (11) s	166 ± 12 s	3 s	Apr 24 s

portion of migrants reported in Table 1 and the pattern of cumulative catch reported in Figure 3 should be viewed with caution.

Steelhead Abundance and Relationships with Pool Features

Juvenile steelhead were observed throughout the lower river main stem during each monthly survey; divers rarely encountered a pool where no steelhead was observed (Figure 5). Dive counts of steelhead in individual pools ranged from 0 to 106 across all months and years. Twenty or fewer steelhead were observed in most (80%) of the 237 pools during the three years, whereas 10 or fewer steelhead were observed in 57% of all pool counts. There were only 11 pools during the three years where no steelhead were observed. For each year and month, abundance estimates for juvenile steelhead (<10 cm TL) ranged from 110 to 1,894 individuals/km of pools, whereas the abundance estimate of steelhead (≥10 cm TL) ranged from 106 to 752 individuals/km of pools (Figure 6). Across all years and months, the average estimated abundances for small and large size-classes of steelhead were 779 and 375 individuals/km of pools.

Counts of juvenile steelhead were related to features of the sampled pools (Table 2). Pool location contributed to the multiple-regression models for predicting counts of both small and large size-classes of steelhead. Standardized regression coefficients between counts of steelhead and pool location were consistently negative, indicating that counts were higher with distance downstream; the highest counts were typically observed downstream of a large tributary (See Canyon Creek, Figure 1). Average depth of the sampled pools contributed to the models for predicting counts of juvenile steelhead, especially for the larger size category of steelhead. Likewise, surface area of the sampled pools contributed to the models for predicting counts of juvenile steelhead. Standardized coefficients for depth and surface area were mostly positive. The month of a particular survey generally did not contribute to the prediction of numbers of steelhead.

Discussion

Characteristics of the Migrants and Migration

That larger juveniles in March were followed by smaller juveniles until early summer is similar to that noted for steelhead in central California (Shapovalov and Taft 1954), Washington (Loch et al. 1988), and Alaska (Thedinga et al. 1991). We documented juveniles migrating downstream during much of the year; however, the largest number migrated in spring along with an apparent secondary migration in late fall or early winter during storm events (Shapovalov and Taft 1954). Timing of peak smolt migration in our study was about 3–4 weeks earlier than the peak migration reported for streams in Washington (Loch et al. 1988) but was within the ‘‘peak run time’’ reported for streams in south-central California (Fukushima and Lesh 1998). Our observation that smolts included fish from a range of lengths is consistent with findings of others in Oregon (Chapman 1958), Washington (Loch et al. 1988; Peven et al. 1994), British Columbia (Ward and Slaney 1988), and Alaska (Thedinga et al. 1991; Bramblett et al. 2002).

In San Luis Obispo Creek, we observed a decline in the number of migrants in late spring and early summer, which corresponded to declining

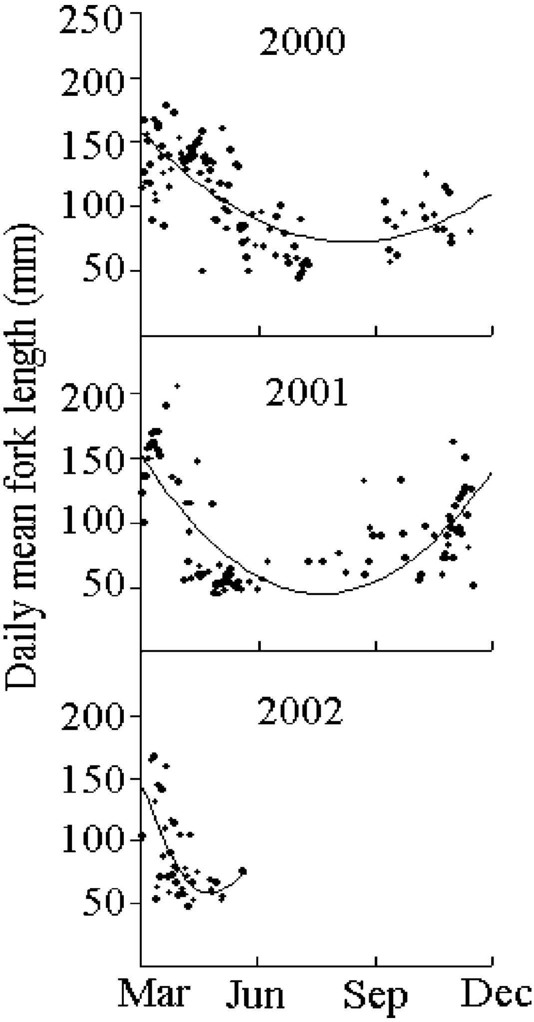

FIGURE 4.—Relationship between daily mean fork length of juvenile steelhead captured in the downstream migrant trap and time of capture (i.e., elapsed time since first date of trapping). The line in each graph was fit with nonlinear regression. The resulting functions are as follows: daily mean fork length = 158 − 0.95 · (day of capture) + 0.003 · (day of capture)^2 for year 2000 (N = 112); daily mean fork length = 151 − 1.4 · (day of capture) + 0.004 · (day of capture)^2 for year 2001 (N = 99); and daily mean fork length = 143 − 2.6 · (day of capture) + 0.02 · (day of capture)^2 for year 2002 (N = 40). Tick marks along the x-axis represent the middle of the indicated month.

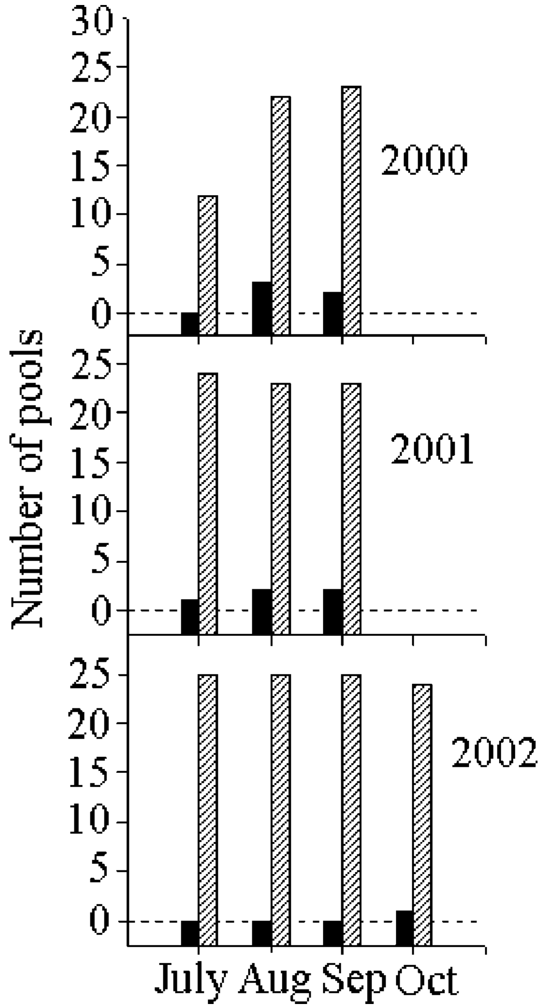

FIGURE 5.—Number of pools where juvenile steelhead were either observed or not observed during dive surveys of the main stem of San Luis Obispo Creek in summer and fall 2000–2002. The October survey was performed only in 2002. The number of pools surveyed (N) in July 2000 was 12; for subsequent surveys, N = 25.

discharge; for streams with relatively high continuous runoff, the number of migrants (mostly smaller individuals) declined later (during August and September; Shapovalov and Taft 1954). In our study, peak captures of steelhead coincided with elevated discharge, which was otherwise low except during and shortly after periods of rainfall. In streams that experience relatively high runoff of long duration, the relationship between spring emigration and discharge might be weak or not detectable (Shapovalov and Taft 1954; Loch et al. 1988). In San Luis Obispo Creek, migration patterns were similar between 2000 and 2001 but were abbreviated in 2002. One factor in 2002 that differed from the previous two years was the extremely low precipitation (and discharge).

The contribution of month to the multiple-regression models for predicting daily catch of ju-

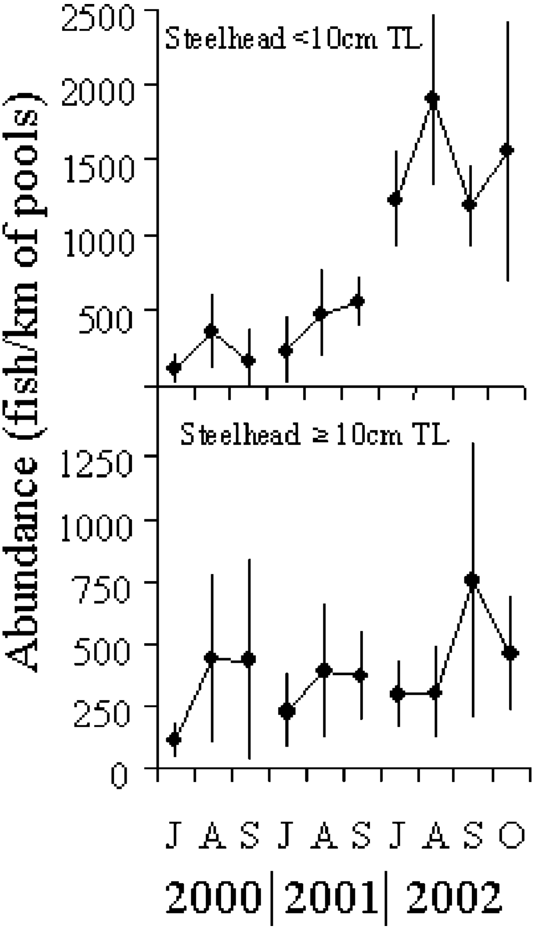

FIGURE 6.—Abundance estimates ±95% confidence intervals for two size-classes of juvenile steelhead in the main stem of San Luis Obispo Creek for four individual months (July, August, September, and October) during 2000–2002. The October survey was performed only in 2002. The number of pools surveyed (*N*) in July 2000 was 12; for subsequent surveys, $N = 25$. The lower confidence limit for the September 2000 abundance estimate of steelhead smaller than 10 cm TL was truncated at zero.

venile steelhead suggests that seasonal environmental factors other than discharge are influencing migration. Besides discharge, temperature and photoperiod vary seasonally; evidence indicates these factors may confine parr–smolt transformation (i.e., seawater readiness) and related migratory behavior to certain times of the year (Adams et al. 1973; Zaugg and Wagner 1973; Wagner 1974), particularly for conspecifics in southern landscapes (McCormick et al. 1999). Temperature and photoperiod may be a plausible explanation for not capturing a smolt after 1 June of any year, though further study is needed to assess the influence of these factors on smolt emigration and seawater readiness in southern territories.

We found that parr mix with smolts, which corroborates and extends the general findings of studies performed in northern parts of the geographic range of steelhead (Alaska: Thedinga et al. 1991; Washington: Leider et al. 1986), and the same is noted for Atlantic salmon *Salmo salar* (Cunjak et al. 1989). Reasons for parr exodus from upstream areas in San Luis Obispo Creek are not known, but may include high-flow events (Harvey 1987) and biotic interactions (Keeley 2001), both of which can displace juvenile fish to downstream habitats. In San Luis Obispo Creek, portions of the upper main stem and tributaries often experience extremely low discharge and intermittent surface flow during summer and even earlier in dry years. Hence, a portion of the downstream migration of parr could be a response to declining rearing conditions (e.g., shrinking living space, increasing water temperature) in upstream areas (Erman and Leidy 1975; Bramblett et al. 2002).

Managers of steelhead in southern landscapes can use our findings as a basis to collaborate with project proponents for the purpose of developing strategies to minimize and mitigate adverse effects on the downstream migration of juvenile steelhead. Anthropogenic activities that possess a likelihood of disrupting the migration should be scheduled for summer or early fall. Because our findings indicate parr are present in the migration and juvenile anadromous salmonids can rear in river main stems (Johnson et al. 1994; Murphy et al. 1989, 1997), scheduling activities to avoid the migration may not evade steelhead entirely. Our finding that the timing and magnitude of the downstream migration was related to estimated discharge suggests that managers of water diversions and reservoirs should consider whether downstream water releases comport with the migration requirements of juvenile steelhead.

Rearing in the Lower Main Stem

Our finding that juvenile steelhead rear in the main stem of a south-central California stream corroborates and extends the findings obtained from studies conducted in Washington (Loch et al. 1988), British Columbia (Hartman and Brown 1987), and Alaska (Johnson et al. 1994; Bramblett et al. 2002). Steelhead parr will emigrate from upstream areas during spring to rear in main-stem habitats (Hartman and Brown 1987; Bramblett et al. 2002), and our findings indicate that steelhead

TABLE 2.—*P*-values and standardized regression coefficients (in parentheses) of the multiple-regression analyses relating counts of small (<10 cm TL) and large (≥10 cm TL) juvenile steelhead (the response) to features of the sampled pools in the main stem of San Luis Obispo Creek in 2000, 2001, and 2002. Location refers to the position of each sampled pool within the main stem and is referenced downstream. Differences in sample size (*N*) are a result of sampling only 12 pools in July 2000 and an additional 25 pools in October 2002.

				Feature			
Year	Response	R^2	*N*	Location (km)	Mean depth (cm)	Surface area (m^2)	Month
2000	Small[a]	0.33	62	0.005 (−0.38)	0.03 (0.24)	0.1 (0.22)	0.9 (−0.01)
	Large	0.54	62	<0.0005 (−0.51)	<0.0005 (0.55)	0.02 (−0.27)	0.06 (0.17)
2001	Small[a]	0.46	75	<0.0005 (−0.54)	0.8 (−0.03)	0.002 (0.3)	0.7 (0.04)
	Large[a]	0.41	75	0.03 (−0.21)	0.005 (0.27)	0.001 (0.35)	0.005 (0.27)
2002	Small[a]	0.51	100	<0.0005 (−0.54)	0.12 (0.12)	<0.0005 (0.4)	0.02 (0.18)
	Large[a]	0.50	100	0.6 (−0.04)	<0.0005 (0.59)	<0.0005 (0.36)	0.4 (0.06)

[a] Data square-root transformed.

in San Luis Obispo Creek engage in a similar spring emigration. This may partially explain our finding that juvenile steelhead were particularly abundant near the mouth of See Canyon Creek. Although surface inflow from this tributary may attract steelhead to the localized area, this will probably not occur during summer because surface inflow is typically nonexistent during the dry season.

Changing environmental conditions in fall (e.g., increasing streamflow, decreasing water temperature) are believed to prompt fish migration to overwintering habitats (Cunjak et al. 1989). Although findings from the October survey indicate that steelhead were relatively abundant, we do not know whether juvenile steelhead are overwintering in the lower main stem. ''Fall freshets'' that are believed responsible for prompting the return of juvenile anadromous salmonids to overwintering areas (Peterson 1982; Tschaplinski and Hartman 1983) did not occur in the San Luis Obispo Creek area until early November 2002 after our fall survey.

The release of treated wastewater in the lower main stem creates and maintains habitat for juvenile steelhead, even when the natural sources of surface water to the lower main stem (i.e., reaches immediately upstream of the effluent outfall and in lower reaches of tributaries to the lower main stem) are dry. The large, deep pools in the lower main stem probably contribute to steelhead survival, especially that of larger juveniles, based on the relationship between the counts of steelhead and mean pool depth (and area) documented in our study and the work of other investigators, suggesting the value of deeper water for larger fish (Harvey and Stewart 1991; Harvey and Nakamoto 1997; Spina 2003). Although we are not aware of all situations where similar releases of treated municipal wastewater in streams are providing habitat for juvenile steelhead, we do know that comparable findings have been documented for Malibu Creek (34°02′05″N, 118°41′43″W; Keegan 1990).

Those who restore the habitat characteristics and conditions needed to further recovery of aquatic environments or imperiled species could conceivably argue for the cessation of treated wastewater releases into coastal streams. Similarly, municipal efforts to conserve the availability of potable water resources could include redirecting treated wastewater to ornamental landscapes, parks, and golf courses. Either of these scenarios may have an undesirable effect on imperiled species in streams where treated wastewater maintains habitat and species abundance that would otherwise not be observed. Determining when the existing release of treated municipal wastewater in coastal streams is necessary or valuable for sustaining imperiled populations over short or lengthy temporal scales is an issue that may eventually confront restoration ecologists and fishery managers.

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