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Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary

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Abstract: To investigate the role that estuaries play in the survival of steelhead, *Oncorhynchus mykiss*, we compared juvenile size at ocean entry with back-calculated measures of size at ocean entry for returning adults in Scott Creek, a representative California coastal stream. During the annual spring emigration, the largest smolts (>150 mm fork length (FL)) move directly to sea, while some smaller smolts remain in the estuary until sandbar formation creates a closed freshwater lagoon. High growth rates in the estuary throughout the summer result in a near doubling of fork length from the time of estuary entry (mean FL of spring migrants = 102.2 mm; mean FL of fall lagoon resident = 195.9 mm). Analysis of the scale morphology of returning adult steelhead indicates that there is strong size-dependent mortality at sea, with estuary-reared steelhead showing a large survival advantage, comprising between 87% and 95.5% (based on tag returns and scale analysis, respectively) of the returning adult population despite being between 8% and 48% of the annual downstream migrating population. Although the estuary forms less than 5% of the watershed area, it is critical nursery habitat, and steelhead population persistence in southern margin ecosystems may well depend upon healthy estuaries.

Résumé : Afin d'estimer le rôle joué par les estuaires dans la survie de la truite arc-en-ciel anadrome, *Oncorhynchus mykiss*, nous avons comparé la taille des jeunes au moment de leur arrivée en mer avec les mesures obtenues par rétrocalcul de la taille des adultes qui reviennent de l'océan au moment de leur propre entrée en mer dans Scott Creek, un cours d'eau côtier typique de Californie. Durant l'émigration annuelle du printemps, les saumoneaux les plus grands (>150 mm de longueur à la fourche (FL)) se rendent directement en mer, alors que certains des saumoneaux plus petits demeurent dans l'estuaire jusqu'à ce que la formation de barres crée une lagune fermée d'eau douce. De forts taux de croissance dans la lagune au cours de l'été produisent un doublement de la longueur à la fourche par rapport au moment de l'arrivée dans l'estuaire (FL moyenne des migrateurs du printemps = 102,2 mm; FL moyenne des résidents de la lagune à l'automne = 195,9 mm). L'analyse de la morphologie des écailles des truites arc-en-ciel anadromes qui reviennent de mer indique une forte mortalité reliée à la taille dans l'océan; les truites élevées dans l'estuaire possèdent un important avantage en ce qui concerne la survie; ils représentent entre 87 % et 95,5 % (d'après respectivement les retours d'étiquettes et l'analyse es écailles) de la population des adultes qui reviennent, même s'ils ne constituaient qu'entre 8 % et 48 % de la population annuelle en migration vers l'aval. Bien que l'estuaire forme moins de 5 % du réseau hydrographique, c'est un habitat de nourricerie important; il est bien possible que la persistance de la population de truites arc-en-ciel anadromes dans les écosystèmes situés à la bordure sud de l'aire de répartition dépende d'estuaires en bon état.

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Introduction

Throughout much of their range, steelhead (*Oncorhynchus mykiss*) populations continue to decline despite federal Endangered Species Act (ESA) listings. This loss has been attributed to habitat degradation, water loss, and poor land management (Nehlsen et al. 1991; Busby et al. 1996). Still, the factors affecting the distribution and dynamics of steelhead populations are not well understood, and few studies have looked at juvenile rearing habitats and their effect on survival for these threatened populations. Because of their anadromous life cycle, salmonids inherently encounter several distinctly different habitats throughout their life history. The contributions of differential habitat use to the growth and survival of individuals may play key roles in their recruitment to adult populations and has been the focus of extensive study for some salmonids (Reimers 1973; Mitro and Zale 2002; Harvey et al. 2005) but largely ignored for steelhead.

During their seaward migration, salmon may enter estuarine habitats, which vary widely in their physical characteristics (Healey 1991). Estuaries are of particular interest because they have been found to be nurseries for many species of fishes and invertebrates (Sogard 1992; Yamashita et al. 2000; Le Pape et al. 2003), allowing juveniles using them to recruit disproportionately to the adult population compared with those from other habitats (Beck et al. 2001). Salmon use of estuarine habitats has been well documented for

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rivers from British Columbia to central California (Levy and Northcote 1982; McCabe et al. 1986; MacFarlane and Norton 2002). However, the time spent in an estuary and the benefits received from that habitat may vary widely among species and watersheds (Bottom et al. 2005). Some salmon move through estuaries in days, whereas others remain for months (Myers and Horton 1982; MacFarlane and Norton 2002; Miller and Sadro 2003). Increased survival of estuarine-reared individuals has rarely been documented (Reimers 1973), although rapid growth in the estuary has been documented for some species and populations (Healey 1979; Simenstad et al. 1982; Fisher and Pearcy 1990*a*).

Estuaries of coastal watersheds in the southwestern margin of North America commonly form ephemeral freshwater lagoons, seasonally closed to the coastal ocean. These lagoons are formed by low summer flow regimes that cannot displace ocean sand deposition at the mouths of the estuaries (Schwarz and Orme 2005). Eventual formation of a sandbar effectively blocks surface connectivity with the ocean and reduces the tidal influence on the system, creating a warmer, mostly freshwater, slow-moving body of relatively deep water. Lagoon conditions generally exist until the first winter pulse of freshwater increases streamflow and removes the sandbar, opening the lagoon to the ocean. The development of lagoon conditions and their effects on salmonids is not well understood. However, a recent study has shown a lagoon environment to be beneficial to the growth of juvenile steelhead in central California (Hayes et al. 2008). Because of their dynamic state and to avoid confusion, lagoon habitats will be referred to as the estuary for the remainder of this text, regardless of its connectivity to the ocean.

Ward et al. (1989) found a strong size-dependent ocean survival in British Columbia's Keogh River steelhead, with the largest smolts (i.e., juveniles migrating to sea) exhibiting a higher survival than smaller migrants. In addition, young steelhead have been observed in estuaries, where growing conditions may be favorable (Dawley et al. 1985; Quinones and Mulligan 2005); however, no research to date has successfully attributed survival of returning adults to estuarine rearing habitat. Higher ocean survival of estuary-reared steelhead would implicate the estuary as an important nursery habitat, especially given the small proportion that it represents of all freshwater habitats. In light of past and current declines of steelhead populations, it is necessary to make the link between individuals that recruit to the reproductive population and the factors that may have lead to their survival.

Here, we determined whether a coastal California estuary serves as a steelhead nursery habitat, producing a disproportionate contribution to adult populations than would be realized in its absence. To address both the importance and mechanism of the estuary as a nursery habitat, we investigated two key questions: (*i*) is there size-related differential marine survival in coastal California steelhead, and if so, (*ii*) do estuarine-reared juveniles experience higher marine survival and recruit to the spawning adult population in greater proportion than individuals that migrate directly to sea with minimal use of the estuary.

To determine the extent to which estuary residence influences the survival rate of steelhead at sea, we sampled both the juvenile and adult steelhead populations over several years (2002–2007) in a typical coastal watershed along the coast of central California. Initially, we estimated the strength of size-dependent ocean survival from a population of hatchery-reared juveniles and adults that were permanently marked (adipose fins removed) as smolts. We then estimated the abundance and size distribution of both the downstream migrating juveniles (both hatchery and wild-spawned smolts) and the subset of downstream migrants that recruited to the estuary and remained there throughout the summer and fall. Sampling of these groups effectively measured both of the dominant steelhead life-history types in Scott Creek: those individuals that move from the upper watershed to the ocean with minimal stay in the estuary and those that move from the upper watershed to the estuary for a period of months before beginning their ocean migration (Hayes et al. 2008). In addition, we used passive integrated transponder (PIT) tags to estimate juvenile-to-adult survival rates of a subset of individuals from both estuarine and upstream habitats. Finally, scale samples were taken from returning adults to identify the size at initial ocean entry and classify the juvenile rearing habitat (i.e., upstream or estuary) through scale morphology (Ward et al. 1989).

Materials and methods

Study site

Scott Creek is a small, coastal California, USA, watershed (~70 km^2) that empties into the Pacific Ocean 80 km south of the mouth of San Francisco Bay (Fig. 1). Large waterfalls form impassable barriers on each of the main tributaries, thereby restricting access by anadromous fish to just 23 km of stream. Flow in Scott Creek is highly variable among seasons and years. Peak winter flows can reach 28 m^3·s^{-1}, whereas summer and autumn flows can be reduced to 0.08 m^3·s^{-1} during an average year and the stream can run dry in the lower reaches during extreme droughts. Substrata throughout the watershed are mudstone and granite with particle sizes ranging from boulder to sand. The upper portion of the watershed is comprised of a high gradient stream dominated by a thick coastal redwood (*Sequoia sempervirens*) canopy. The lower gradient main stem of the creek has a low-density overstory cover composed of alders (*Alnus* sp.), with understory dominated by willows (*Salix* sp.). An area of low-lying stream near the ocean forms a small estuary, which is subject to periods of high salinity during large tidal and swell events. The estuary is surrounded by a bullrush (*Scirpus californicus*) marsh. Like many coastal California streams, a sandbar forms most summers, causing the estuary to become a freshwater lagoon with infrequent saltwater input from ocean swells and tides. These environmental features (i.e., the geomorphology and riparian vegetation) that characterize the Scott Creek watershed are representative of many coastal streams along central and northern California.

Fishes of Scott Creek include steelhead, coho salmon (*Oncorhynchus kisutch*), threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), coastrange sculpin (*Cottus aleuticus*), and tidewater goby (*Eucyclogobius newberryi*). Juvenile starry flounder (*Platichthys stellatus*) and Pacific staghorn sculpin (*Leptocottus armatus*) are infrequently observed in the estuary.

A small conservation hatchery has operated continuously on Scott Creek since 1982, spawning a small number of

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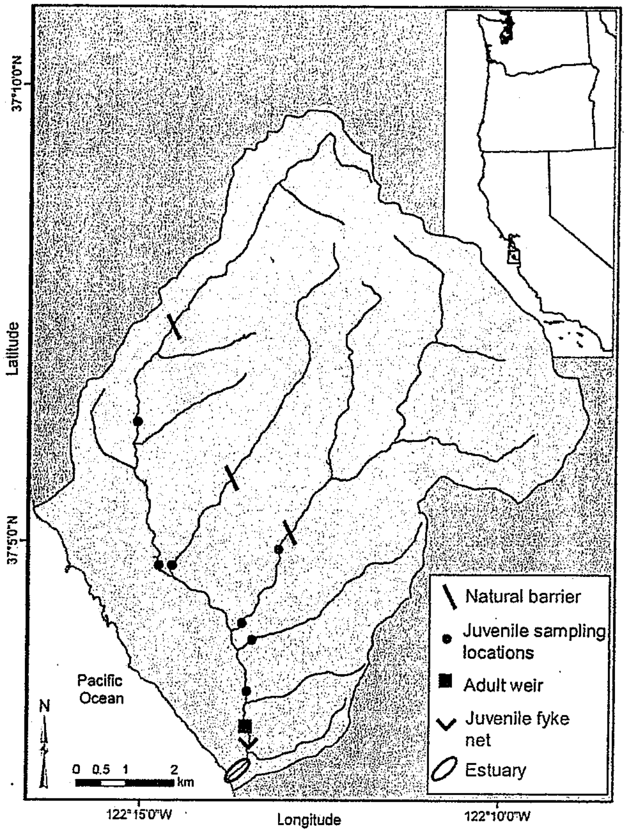

Fig. 1. Map of the study site in Scott Creek watershed. Inset shows location in California on the US West Coast.

steelhead and coho salmon each spring from broodstock that are at least one generation removed from the hatchery (Hayes et al. 2004). Like many southern populations, steelhead in Scott Creek are listed as threatened by the ESA because of low population numbers, despite a relatively unaltered watershed.

Size-selective survival

To test for size-dependent survival of steelhead at sea, we compared the initial size distribution of a cohort of smolts as they migrated to sea with the juvenile size distribution of returning adults of that cohort when they returned to Scott Creek. For this, we used a population of marked (adipose fin permanently removed) hatchery-reared smolts released in the spring of 2003. Hatchery smolts enter the ocean soon after release; therefore we assume that the size distribution of hatchery fish prior to release closely resembled the distribution of smolts that migrate directly to sea (Hayes et al. 2004). We measured the fork length (FL; to the nearest millimetre) of 562 hatchery-raised smolts from the entire pool of 6880 individuals, 1 week prior to release from the hatchery. Size at ocean entry was determined for the adults of this hatchery-reared cohort when they returned in the winter and spring of 2004 and 2005 as 1- and 2-ocean-year fish using the scale method described below. The size distribution at release of hatchery smolts was compared with the back-calculated size at ocean entry of returning hatchery adults to determine whether processes of size-dependent ocean survival have an effect on the resulting adult population. The probability of steelhead straying to Scott Creek from other streams is extremely low (Shapovalov and Taft 1938), and all adults captured were assumed to be of Scott Creek origin for the purposes of our analyses. Hatchery adults that returned from the ocean in the winters and springs of 2004–2006 to spawn were sampled with a floating resistance panel weir, operated daily during the spawning run (Hayes et al. 2004). The weir had a trap box with a one-way door to capture steelhead moving upstream. Upon capture, each fish was identified as either of hatchery (n = 278) or of wild (n = 590) origin and was measured to the nearest 0.5 cm FL and weighed to the nearest 0.1 kg. A sample of 10–15 scales was taken from just above the lateral line on a diagonal between the posterior attachment of the dorsal fin and the anal fin (Maher and Larkin 1955).

To determine the size at ocean entry of surviving hatchery adult steelhead from the 2003 smolt class, we used the linear relationship between fish size and scale size (Ricker 1992) and the reliable changes in scale morphology that are associated with changes in growth and habitat (e.g., ocean entry checks, circuli spacing with growth). Scales were cleaned with deionized water and photographed using a microscope-mounted Nikon® digital camera (DXM1200 3840 × 3072 pixels). The most original, uniform scale from each fish was photographed and saved in the tag image file format (TIFF).

Once each scale had been photographed, OPTIMAS® software (version 6.5; Media Cybernetics, Inc., Silver Spring, Maryland) and a custom macro were used to analyze for total scale radius (SR, the distance from the focus to the edge of the scale), radius at ocean entry (OER, the distance from the focus to the ocean entry check), number and spacing of each freshwater and ocean circulus, and number of ocean annuli (Fig. 2). For ease of reading, all measurements were made 20° off the longest axis. A qualitative score for each analysis was noted with a rank of 1 to 3, with 1 being a very original (i.e., the scale has remained on the fish since scales were formed and has not been lost and regenerated), normally shaped scale with a high reading confidence. Only scales with a score of 1 or 2 were used in further analyses.

FL at the initial ocean entry check was back-calculated on scales from adult steelhead using a regression of FL on total scale radius (SR). A linear regression was created with original scales from 1251 juvenile and adult Scott Creek steelhead representing the complete range of sizes available. The relationship between SR and FL (Fig. 3) is described by

$$(1)\qquad \text{FL (mm)} = 0.1686\text{SR } (\mu\text{m}) + 34.872 \quad (R^2 = 0.97)$$

An intercept of 34 mm is similar to other published values of FL at initial scale formation for *O. mykiss* (Snyder 1938; Kesner and Barnhart 1972; Hopelain 1998). There is some discussion in the literature as to the most appropriate method for back-calculation of size (Panfili and Troadec 2002); however, the Fraser–Lee method is widely used, and recent studies have empirically demonstrated its reliability in several fish species, including *O. mykiss* (Davies and Sloane 1986; Klumb et al. 1999). We employed the Fraser–Lee method (Fraser 1916; Lee 1920) in all back-calculations of fish length. Briefly, the Fraser–Lee method utilizes the relationship between fish length and scale radius at time of

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Fig. 2. Photograph of scale indicating (*a*) focus, (*b*) ocean entry radius (OER), and (*c*) scale radius (SR) and the 20° offset from the center axis used to make measurements.

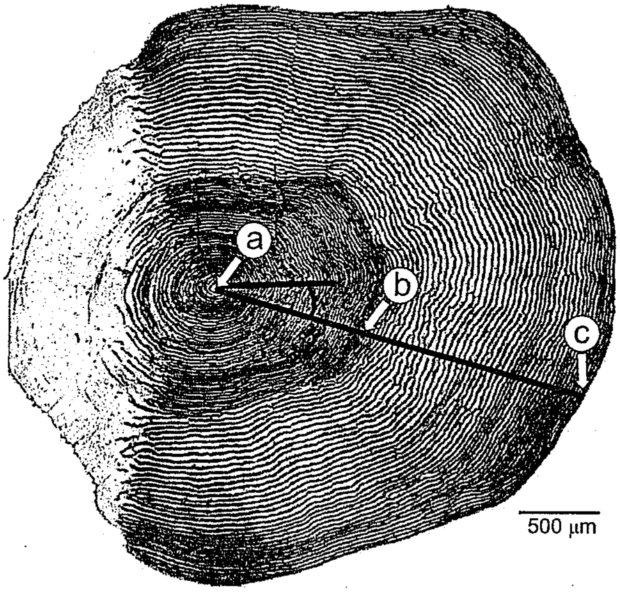
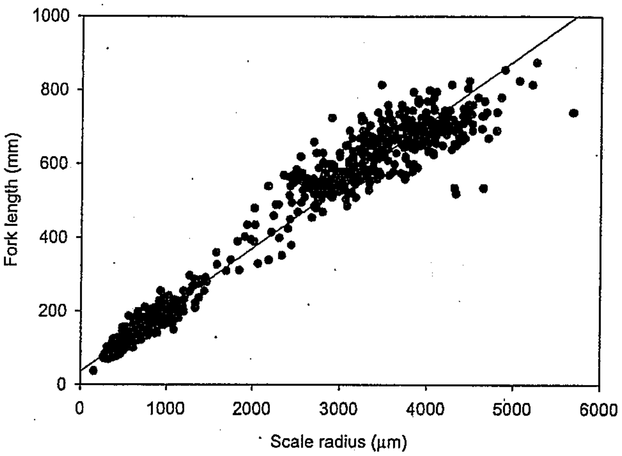


Fig. 3. Relationship between fork length (FL) and scale radius (SR) based on scales from juvenile and adult steelhead (*Oncorhynchus mykiss*) collected throughout the watershed from 2002 to 2005 (n = 1250, FL = 0.1686 SR + 34.87, R^2 = 0.97).



capture to determine fish length at any radius along the scale when adjusted by the intercept of a fork length on scale radius regression for the species in question (Klumb et al. 1999).

Size at ocean entry of estuarine-reared juveniles

To determine whether juvenile steelhead reared in strictly upstream habitats and the subset of those fish that remained in the estuary for an additional 6–9 months entered the ocean at different sizes and numbers, we trapped downstream migrants (smolts) each spring and summer and sampled the estuary population each fall (October–December). To determine the number and size of downstream migrants, we placed a fyke net across the stream approximately 50 m upstream of the estuary (Fig. 1). The fyke net (initial mesh size in 2002–2003 was 9.5 mm, switching to 6.4 mm in 2004 because of the small size of many migrants) was generally operated three days per week, January–July (2002–2005); however, storm events periodically prohibited the net from being operated. The number of downstream migrants was estimated by adjusting total fish captured (n = 1722) by capture efficiency (Hayes et al. 2004).

Captured steelhead were measured to the nearest millimetre FL, and mass was measured to the nearest 0.01 g. A sample of 10–15 scales was taken by running the blade of a pair of scissors in the posterior to anterior direction lightly along the side of the fish. Finally, each fish ≥65 mm FL was scanned for a PIT tag, using a handheld tag reader (Allflex USA, Dallas Fort Worth Airport, Texas). If no tag was found, then one would be injected (n = 1038) using a sterile 12-gauge needle.

The estuary habitat was sampled each fall (2002–2005) to determine the population size and the size distribution of juvenile steelhead that inhabited the estuary just prior to ocean entry (referred to as "estuary juveniles"). The estuary habitat, defined as the area from the beach at the mouth of Scott Creek to approximately 800 m upstream (Fig. 1), was sampled using a 30 m × 2 m nylon beach seine. The entire estuary was seined as thoroughly as possible in 50 m sections, with the exception of the upper 200 m, where dense willow cover made seining impossible. All fish (n = 392) were placed into mesh containers in the estuary until all seining was complete so that fish were not collected twice. Estuary juveniles were assessed using the same protocol as trap-captured downstream migrants. However, the estimation of size at ocean entry required adjusting the size distribution of the last sampling each fall to account for growth occurring between the last sampling and sandbar breakage such that growth rates from the last sampling event (see Hayes et al. 2008) and the number of days between the last sampling and bar breakage were calculated and added to the final fall size distribution. Because of changes in sampling equipment and varying trap effectiveness among years, distributions could not be compared statistically among years, necessitating the grouping of juveniles into two distributions: spring downstream migrants (i.e., those fish that move from upstream habitats to estuarine and ocean habitats each spring) and fall estuary juveniles (i.e., the subset of spring downstream migrants that did not move to the ocean but remained in the estuary throughout the summer, as measured in the fall).

To explore those processes that might determine which fish remain in the estuary prior to migration to sea, we examined whether size at migration or timing of migration affected individuals present in the estuary after bar closure. To do this, we compared the size distribution of all downstream migrants with the size distribution at downstream migration of those PIT-tagged individuals that stayed in the estuary after sandbar closure. Data were organized into 15 mm FL bins from 85 to 145 mm, with all fish greater than 145 mm being grouped into the last bin of >145 mm. To determine what effect timing of downstream migration had in determining what individuals remained in the estuary by sandbar closure, we compared the trapping date for all

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fish tagged at the downstream migrant trap with the initial tagging date for those that remained in the estuary.

Effect of estuarine residence on recruitment to the adult population

We used three methods to determine whether estuary fish recruited disproportionately to the returning adult population. First, we calculated the size at ocean entry of returning adults and compared that distribution with the sizes at ocean entry of emigrating juveniles. Second, we classified returning adults to either upstream or estuary juvenile rearing habitat using maximum likelihood estimation and measures of scale morphology. Finally, we calculated return rates of adult steelhead that were PIT-tagged as juveniles at one of the two habitats to determine relative return rates for each habitat type.

We back-calculated the size at ocean entry of wild returning adult steelhead with the same scale measurement technique that was employed for returning hatchery fish. Scale samples were collected from 571 wild adults from spring of 2002 through spring of 2006. Although some 1-ocean-year fish were captured in 2006 and assigned to the 2005 ocean entry group, these samples were omitted from this analysis because of the potential bias of using only "early" returning fish to classify the entire 2004 cohort. In addition, scales with visible spawning checks (i.e., an area of degradation in the scale from previous stream entry) were removed to ensure that no fish was counted twice. After removals, 406 original, uniform scale samples that received a score of 2 or better during reading were used for the final analysis. Because of the difficulties in identifying freshwater annuli in adult scales, especially in estuary residents, returning adult steelhead were not assigned to a particular downstream migrant cohort for comparison. Instead, all returning adults were grouped together as one class, and their ocean entry FL was compared with the FL of fall estuary-reared fish and spring downstream migrants from all years. Unfortunately, trapping fish as they cross the sandbar to enter the ocean is not currently feasible, and size at ocean entry of fish that do not utilize the estuary must be inferred from the population that remains. This is difficult because of the potential, currently unknown, size-selective effects of predators during the migration. Fish not found in the estuary may have either gone to sea or been consumed by predators between the trap and the ocean. In this scenario, the most conservative comparison is to compare all spring downstream migrants and all fall estuary steelhead with the size distribution at ocean entry of the surviving adult population.

In addition to size, we used circuli spacing and spacing variance to distinguish between adults with significant juvenile estuarine rearing time and those that moved to sea without utilizing estuarine habitats. Circuli spacing (i.e., the width of the increment between adjacent circuli) in scales is correlated with growth in coho salmon (Fisher and Pearcy 1990*b*, 2005), sockeye salmon (*Oncorhynchus nerka*) (Fukuwaka and Kaeriyama 1997), and steelhead for which the origin of fish in mixed stocks of hatchery and wild steelhead has been determined and differences in circuli spacing attributed to the different growth regimes in the hatchery and the wild (Maher and Larkin 1955; Bernard and Myers 1996; Tattam et al. 2003). Upstream scales were collected throughout the year in the upper watershed, but because individuals only use estuary habitat after a prior stay in the upper watershed, estuary scales were taken in the late fall when the estuary growth signature has been maximized. To provide an indication of estuary-derived growth, we calculated the mean of log-transformed circuli spacing and variance for the last 18 circuli of juvenile fish of all size classes from the upper watershed ($n = 96$) and estuary ($n = 92$) for use in a discriminant function analysis (DFA). Although many combinations of circuli were tested in a stepwise fashion, the mean of the last 18 circuli (approximately 8–12 months of growth) was most effective at discriminating between prior habitat use, while simultaneously removing problems of non-independence in sampling. A maximum likelihood estimation (MLE) was then used to determine the composition of returning adult steelhead that reared in one of the two juvenile rearing habitats (upstream or estuary) based on the same parameters used in the juvenile DFA (mean log-transformed spacing of the last 18 circuli, variance of spacing). The maximum likelihood analysis results were produced with the program HISEA (Millar 1990).

To calculate the relative ocean survival of wild juvenile steelhead, we placed PIT tags in steelhead at both the downstream migrant trap and the estuary in the spring and summers of 2003–2005. Fish tagged at the downstream migrant trap and subsequently observed in the estuary after sandbar closure were removed from the trap population and added to the estuary population. We then scanned each returning adult for a PIT tag that could be attributed to deployment during one of these years and locations. Return data were used to calculate relative survival of individuals from each group.

Results

Size-selective survival

Hatchery smolts released in April of 2003 experienced strong size-selective mortality at sea (Fig. 4). Smolts measured just prior to release had a mean FL of 158 mm (standard deviation (SD) = 35). Original scales were obtained from hatchery fish returning as adults in the winter–spring of 2004 and 2005 as 1- and 2-ocean-year fish, respectively. Back-calculation of FL at ocean entry indicated that the surviving adult population had a mean FL at ocean entry of 181.2 mm (SD = 28.9), which was significantly larger upon ocean entry than the initial population of fish released from the hatchery ($t_{[592]} = 4.47$, $p < 0.001$).

Size at ocean entry of estuarine-reared juveniles

In 2003 and 2004, there were far fewer estuary fish than downstream migrants (48% and 8% of downstream migrant population, respectively) (Table 1). No population size was estimated for 2002 or 2005 because of the lack of early season samples due to excessive streamflow. Size distribution varied by sample site and year (Table 2), with the estuary residents being consistently larger than downstream migrants. The decrease in size after 2003 in both areas is likely attributable to switching to a smaller mesh net.

The size distribution of the estuary population upon bar breakage each winter varied by year; mean FL upon winter sandbar breakage was largest in 2003 at 213 mm (SD = 32)

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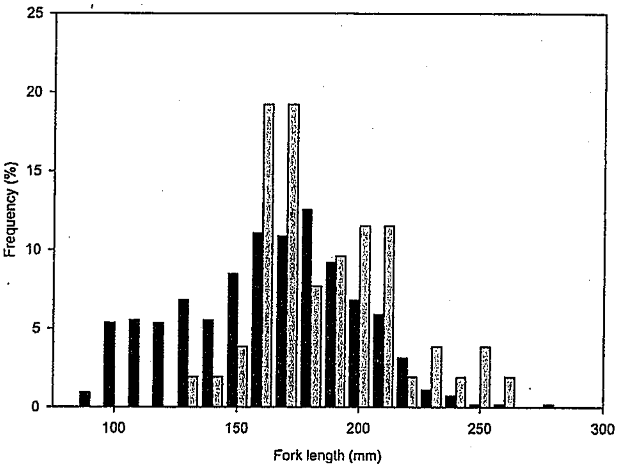
Fig. 4. Size distributions of juvenile hatchery-reared smolts (n = 542, solid bars) sampled immediately preceding release and the back-calculated size at ocean entry of surviving adults from the same cohort (n = 52, shaded bars). Bins are 10 mm.



and smallest in 2004 at 182 mm (SD = 26), but estuary fish from all years (2002–2005) were significantly larger than spring downstream migrating juveniles in the same years ($t_{[455.4]} = 45.76$, $p < 0.001$).

Of the 298 fish that we measured and PIT-tagged at the downstream migrant trap in spring of 2003, 61 were recaptured in the estuary in the fall, well after sandbar formation. The FL at initial estuary entry was compared between the two groups to determine whether specific size classes were more likely to remain in the estuary (Fig. 5). The initial size of all downstream migrants was larger than the initial size of those individuals that remained in the estuary ($\chi^2_{(5,n=359)} = 15.36$, $p = 0.009$), indicating that larger individuals moved directly to sea, whereas some of the smaller individuals remained to populate the estuary after sandbar formation. No fish with an initial estuary entry FL larger than 150 mm was observed after sandbar closure, indicating that those larger fish moved on to the ocean before sandbar formation.

Habitat-specific recruitment to the adult population

To determine whether juveniles that remained in the estuary contributed disproportionately to the subsequent recruitment of returning adults, we compared the size at ocean entry of juveniles from 2002–2005 that either migrated directly to sea or remained in the estuary with the back-calculated size at ocean entry of adults returning in the same years (Fig. 6). For all sampling years combined, FL at ocean entry differed significantly among the spring downstream migrants, fall estuary residents, and back-calculated returning adults (analysis of variance (ANOVA), $F_{[2,1802]} = 2192.9$, $p < 0.001$). Post-hoc comparisons using the Tukey test indicated that there were significant differences among all three groups. The mean FL of spring emigrating smolts for all years was 102.2 mm (SD = 26, n = 1722), whereas the mean FL of fall estuary fish was 195.9 mm (SD = 28, n = 392), and ocean entry FL of returning adults was 208 mm (SD = 38, n = 406).

To provide another independent measure of the effect of juvenile rearing habitat on returning adult steelhead, we used measures of scale spacing as a proxy for juvenile growth, with larger spacing (i.e., increment widths between adjacent circuli) indicating faster growth. Mean spacing was significantly greater in juveniles that occupied the estuary than in those that did not ($t_{[186]} = 13.95$, $p < 0.001$; Fig. 7). We were able to assign juveniles to their respective rearing habitat; DFA jackknifed classification, using circuli spacing and variance as predictors, indicated an 86% correct assignment (90% for upstream, 83% for estuary) to either habitat. Scales from adult fish (n = 406) were also analyzed to determine the mean spacing and variance for the last 18 circuli prior to ocean entry. Spacing was significantly wider than either the estuary or upstream individuals ($F_{[2,593]} = 151.8$, $p < 0.001$). A MLE using mean log-transformed circuli spacing and variance of spacing as predictors indicated that 95.5% and 4.5% of returning adults had reared in the estuary and upstream waters, respectively.

Table 1. Proportion of downstream migrating juvenile steelhead residing in the estuary in 2003 and 2004.

	Year	
	2003	2004
Estimated total no. of wild downstream migrants	5272*	18 354
Estuary population ± SD	2540±479.4	1489±381.9
Downstream migrants utilizing the estuary (%)	48	8

*2003 is assumed to be an underestimate of the wild population due to the large net mesh size used in downstream migrant trapping. Data are from Hayes et al. (2004) and S.A. Hayes, unpublished data.

The strength of differential ocean survival of PIT-tagged estuary- and upstream-reared steelhead was estimated from adults captured in the weir from the winter of 2004 through the spring of 2007. To date, 52 wild steelhead have returned from the ocean carrying PIT tags implanted either at the downstream migrant trap or in the estuary. All fish were tagged as juveniles from 2003 through 2005. In those years, 1260 juveniles were tagged at the downstream migrant trap; however, 169 of these were later observed in the estuary and were removed from the trap totals, leaving a final count of 1091 fish tagged at the downstream migrant trap. A total of 1053 fish were tagged or observed in the estuary after sandbar formation. Forty-five of 52 returning adults were from the estuary juvenile pool, whereas only seven were from the downstream migrant trap. After adjusting for juvenile tagging effort, captures to date indicate that approximately 87% of returning adult steelhead are products of lagoon rearing, whereas 13% were from exclusively upstream habitats.

Discussion

This study provides compelling evidence for the importance of estuarine habitat as a nursery to coastal California steelhead populations. Although estuaries have been shown to function as nurseries for other fish species (Epifanio et al. 2003; Brown 2006), their effect on the relative survival of steelhead was previously unknown. A strong size-selective ocean survival coupled with a large dichotomy in sizes between estuary- and upstream-reared smolts has led to a survival advantage for the larger estuary-reared individuals.

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Table 2. Comparison of the mean size (fork length (FL)) of downstream migrant juvenile steelhead sampled in spring with that of estuary resident juvenile steelhead sampled in both the late spring and fall of each year.

		Downstream migrants		Estuary residents			
				Late spring		Fall	
Year	Trapping dates	*n*	Mean FL (mm) ± SD	*n*	Mean FL (mm) ± SD	*n*	Mean FL (mm) ± SD
2002	April–July	398	110.2±25	19	112.9±12	44	196.2±21
2003	January–July	448	110.0±29	17	108.6±13	81	213.6±32
2004	January–July	665	92.6±24	51	112.1±39	148	182.5±26
2005	March–July	211	96.0±25	102	91.7±38	119	191.1±33
All years		1722	102.2±26	189	106.3±26	392	195.9±28

Fig. 5. Comparison of size distributions of spring downstream migrants passive integrated transponder (PIT)-tagged prior to estuary entry (*n* = 298, solid bars) and the size at initial estuary entry of tagged fish recaptured in the estuary after sandbar closure (*n* = 61, shaded bars). Bins are 10 mm.

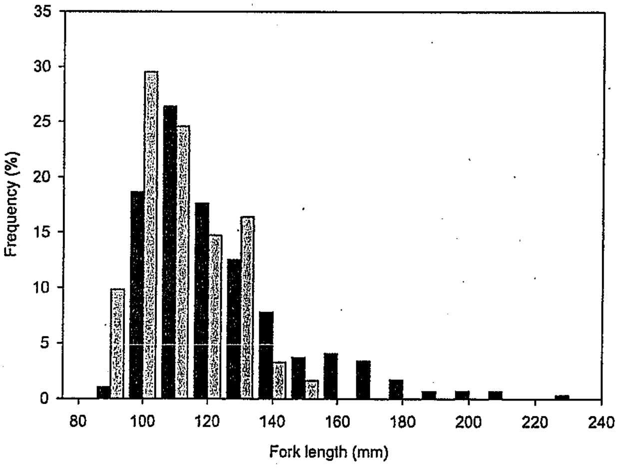
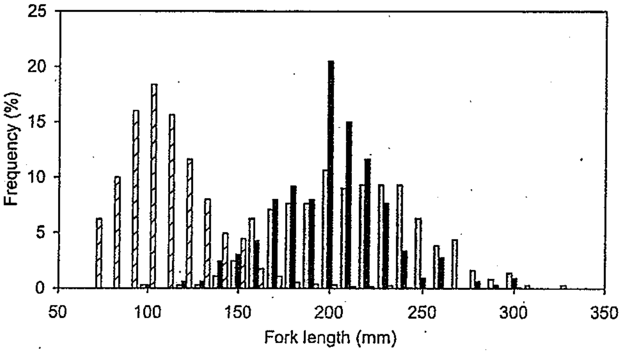


Fig. 6. Summed size distribution of all downstream migrants in 2002–2004 (*n* = 1300, hatched bars), late fall estuary residents in 2002–2005 (*n* = 327, solid bars), and back-calculated size at ocean entry of adults returning in 2002–2005 (*n* = 364, shaded bars). Bins are 10 mm.



These patterns are driven by the difference in growth rates between productive estuary waters and the relatively oligotrophic upstream habitat (Hayes et al. 2008). As most of the estuaries along the California coast have suffered anthropogenic impacts (e.g., channel modifications for buildings, bridges, agriculture, and water diversions), this is likely to have played a major role in steelhead declines in California in the last century (Busby et al. 1996).

Although evidence of size-selective survival in fishes is not new (Sogard 1997), the strength of size-selective survival combined with an extreme dichotomy in sizes of ocean entry between the two general rearing habitats (upstream and estuary) could lead to size-selective survival being the largest determinant in driving which individuals ultimately contribute to the adult population. Back-calculated size at ocean entry for 2003 hatchery juveniles returning as adults in 2004 and 2005 indicated that small smolts (≤150 mm FL) were underrepresented in the returning adult population, and larger smolts (>200 mm) were overrepresented. These data support the size-biased survival proposed by Ward et al. (1989) for a northern stock of steelhead. It has been shown that hatchery-reared salmon may experience lower overall survival in the marine environment (Jonsson et al. 2003); however, the processes shaping the size distribution of surviving fish (i.e., predation, foraging success) should act similarly on both hatchery and wild populations. This would suggest that wild Scott Creek smolts also experience a strong size-biased survival, with the largest fish returning in much greater numbers than those moving to sea at a smaller size. Indeed, our observations of few fish less than 150 mm FL at ocean entry (back-calculated) returning as adults, despite the vast majority of downstream migrating fish in the <150 mm FL size class, further suggests the size-selective survival of wild fish. This apparent 150 mm FL survival threshold is in agreement with a size-selective survival estimate for a northern steelhead population in which survival of smolts below 150 mm was near zero (Ward and Slaney 1988), suggesting that common ocean selection patterns exist across steelhead populations. The basis for reduced survival of the smaller fish remains unclear, but it is likely that the smaller individuals are more susceptible to starvation (Simpkins et al. 2004), predation, and disease (West and Larkin 1987; Becker et al. 2005).

Spring downstream migrants enter the Scott Creek estuary at a relatively small size compared with smolting steelhead in more northern populations (Ward and Slaney 1988; Ward et al. 1989). This is consistent with the relatively low growth rates observed in upstream habitats of Scott Creek (Hayes et al. 2008) and the large numbers of small downstream migrants observed by Shapovalov and Taft (1954) in nearby and physiographically similar Waddell Creek. Although the estimated number and mean size of down-

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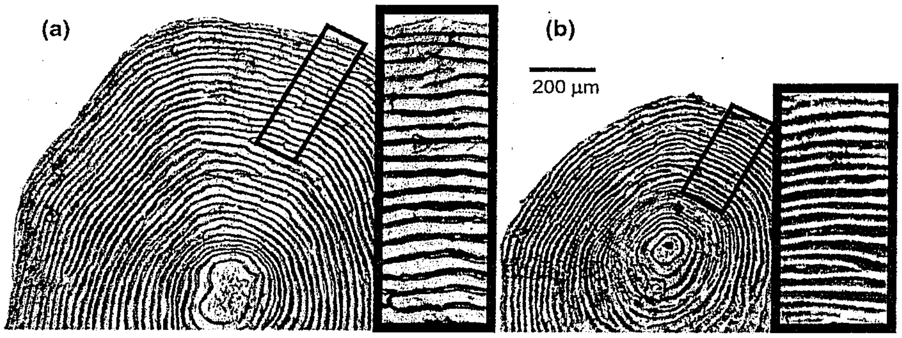
Fig. 7. Comparison of representative scales from juvenile steelhead from (*a*) estuarine habitat (170 mm fork length (FL), mean spacing of last 18 circuli = 27.9 μm) and (*b*) upstream habitat (158 mm FL, mean spacing of last 18 circuli = 2.5 μm). Inset for each scale is an enlargement of the last 18 circuli used in the discriminant function analysis (DFA) and illustrates the difference in mean spacing among fish from estuarine and upstream habitats.



stream migrants differed annually in this study (due to a change in net mesh size), these differences tended to overestimate size at downstream migration. The results still conservatively indicate that the vast majority of Scott Creek steelhead move downstream at a size that is detrimental to marine survival. Many studies have discounted small migrants that do not possess typical smolt physical characteristics (e.g., low condition factor, silver coloration, black tail) as migratory parr that do not enter the marine environment. In southern populations, however, many of these individuals have elevated gill $\mathrm{Na^+/K^+}$-ATPase activity, a common indicator of seawater readiness (C.V. Hanson, unpublished data), and appear to enter the ocean at a small size.

The estuary population of steelhead is comprised of juveniles that emigrated from the upper watershed in the spring and summer. Downstream migrants greater than 150 mm FL move through the estuary and are not observed again as juveniles, suggesting they are large enough to compete successfully in the ocean. Large fish moving directly to sea may also help to explain why the hatchery fish, generally released at double the FL of wild downstream migrants, are rarely observed in the estuary. Most steelhead in Scott Creek appear to be migrating at smaller sizes specifically to benefit from greater estuary growth potential, thus allowing them to enter the ocean at a favorable size and younger age than those reared exclusively in upstream waters (Hayes et al. 2008). The estuary population each fall varied between 8% and 48% of the estimated total number of downstream migrants (in 2004 and 2003, respectively); however, the 48% estuary utilization in 2003 is probably a substantial overestimate (again due to large mesh size passing smaller fish, effectively underestimating the number of downstream migrants). Timing of sandbar formation does appear to impact the overall number of downstream migrants that will reside there. In years when high flow prevents early season sandbar formation, productive deep water is not found until the late summer and may harbor fewer fish. On the other hand, early sandbar formation during low flow years leads to productive habitat being available during peak downstream migration and may cause more fish to remain in the estuary throughout the summer. These considerations suggest that future year-class strength may be due, in part, to the timing of sandbar formation.

It is possible that estuary mortality is low in Scott Creek, which would favor juveniles using the estuary before entering the ocean. Unlike larger estuaries, no marine mammals have been observed in the Scott Creek estuary, and in its closed state, aquatic predators are prevented from entering from the ocean. Prickly sculpin have infrequently been observed feeding on smaller steelhead in the upper watershed; however, most steelhead entering the estuary are probably large enough to avoid predation by prickly sculpin. Avian predators are an important source of estuarine mortality for some salmonids, particularly steelhead in the Columbia River, with birds consuming greater than 10% of the steelhead previously detected moving into the estuary (Ryan et al. 2003). Avian predators (e.g., cormorants (*Phalacrocorax auritus*), brown pelicans (*Pelecanus occidentalis*), gulls (Laridae)) are often present in the Scott Creek estuary but their relative impact is unclear as the deeper estuarine water may provide a refuge from the avian predators (e.g., mergansers (*Mergus* sp.), kingfishers (*Ceryle alcyon*), great blue herons (*Ardea herodia*)) that readily feed on steelhead in the shallower upstream waters. Further study is required to determine what impact predation by seabirds has on the distribution and density of steelhead in the estuary. It is certainly possible, though, that steelhead evolved to utilize the Scott Creek estuary specifically because of the excellent growth opportunity and the relatively low predation pressure compared with marine environments. However, there are likely risks associated with estuarine rearing, otherwise the larger downstream migrants, which tend to pass through, might be expected to stay and increase their chances of marine survival associated with additional growth. These risks include intolerable summer water temperatures, loss of habitat from drought, the intrusion of anoxic saltwater layers and sediments, and predation, any of which may lead to high estuary mortality. In addition, strong density-dependent growth rates could cause fish to enter the ocean upon sandbar breakage at a smaller than optimal size in years of high lagoon steelhead densities (Hayes et al. 2008). It is also unclear when estuary-reared juveniles move to sea. Juveniles moving to sea immediately upon estuary sandbar breakage would experience further selection pressure from ocean conditions, which may be poor in the winter when breakage often occurs. Therefore, juvenile steelhead condition (e.g., size, energy stores) coupled with timing of ocean entry may be a major factor driving demography of the adult population (Limburg 2001).

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As a whole, small coastal estuaries in central and southern California appear to function much differently than larger estuaries (e.g., Columbia River, San Francisco Bay). Many of the larger estuaries have extensive populations of large piscivorous fish (e.g., flatfish (Pleuronectiformes), cutthroat trout (*Oncorhynchus clarki*), striped bass (*Morone saxatilis*)), and potentially vast communities of competitors (e.g., other salmonids (*Oncorhynchus* sp.), perch (Percidae), shad (*Alosa sapidissima*), smelt (Osmeridae), sole (Soleidae)) where extended residence in these areas may not offer the same advantages that smaller estuaries with few other fish species provide.

Back-calculation of size at ocean entry from the morphological characteristics of scales of returning adults indicates that surviving adults were quite large as juveniles upon ocean entry. In fact, the vast majority of survivors were so large at ocean entry that the upstream waters alone could not have produced them, as indicated by the size of downstream migrants. Size-selective survival in both wild and hatchery fish indicates that small fish are less likely to survive in the marine environment and estuary-reared juveniles constitute most of the returning adult population. Using MLE, we determined that over 95% of adults returning from 2002–2006 were at least partially reared in the estuary as juveniles. In addition to habitat assignment through MLE, the comparison of spring smolt versus fall estuary-reared size distributions to back-calculated size at ocean entry of adults gives an independent measure of habitat use that emphasizes the estuary as having been used by most surviving adult steelhead as juveniles. The estuary fills the role of an important nursery in this system by its disproportionate contribution to the adult population that returns to spawn. Unlike some nurseries, however, estuarine rearing requires the migration of fish from the upper watershed and cannot function as the sole rearing habitat for juvenile steelhead. Loose gravel with consistent flow, found only in the upper watershed, is required to incubate steelhead eggs. In addition, the benefits of the estuary habitat observed in the spring, summer, and fall months may not be present in the winter when large flows scour the estuary, leaving little refuge, and potentially disturb anoxic sediments.

The vast majority of the PIT-tagged adult steelhead returning from the ocean were originally tagged or observed in the estuary (87%). Returns of trap tagged fish were poor (13%). Although it is possible that some trap fish moved to the estuary and remained unobserved throughout the summer, adult returns of trap fish should reflect this with higher return rates than we have observed. We feel that these data are in strong agreement with the scale morphology analysis and lend further support to our stance that the estuary is functioning a nursery for young steelhead.

Our study has shown that estuarine rearing is a significant contributor to steelhead population persistence. The results of this study indicate there is size-selective ocean survival of central California coastal steelhead. Further, our results strongly suggest that the estuary is an important nursery habitat for producing large juvenile steelhead with increased ocean survival. Heavy alteration of the Scott Creek estuary from highway development in the 1930s has left the estuary substantially smaller than its historic size and may have drastically altered the hydrodynamics of the system. Estuarine waters in Scott Creek now comprise less than 5% of the habitat available to steelhead, yet the vast majority of the adult population is a product of that environment. Anecdotal estimates of run sizes from Scott Creek prior to highway development suggest spawning adult numbers two to three times larger than those observed today (e.g., California Department of Fish and Game 1910). More work is needed to determine what strategies steelhead utilize in watersheds without estuaries to achieve a size large enough to survive at sea without the additional growth that these habitats afford. Finally, the strength of size-selective mortality in the ocean appears to be sufficient that the very small size at ocean entry for many Scott Creek smolts would eliminate them from the population. Hayes et al. (2008) observed density-dependant growth rates among years for steelhead in the Scott Creek estuary, indicating that there may be a spatial limit on how many fish can recruit to the estuary in some years. Thus, more work is also needed to determine the consequence of increasing the size and duration of estuarine habitat on the size and dynamics of steelhead populations and how density-dependent processes influence these relationships.

These results indicate that coastal estuaries, which are often the most impacted parts of a watershed, may be more important to steelhead persistence in the southern portion of their range than previously thought and that their degradation could have drastic implications for imperiled steelhead populations. Indeed, future efforts to protect and restore steelhead populations in small watersheds should prioritize healthy and sizeable estuarine habitat as an effective method of returning steelhead to their historic numbers. In addition, northern stocks may come to rely on the added resiliency that healthy estuaries provide, as perturbations from habitat alteration or climate change alter the function of traditional rearing habitats.

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