California Fish and Game 101(4):241-266; 2015

Importance of the stream-estuary ecotone to juvenile coho salmon (*Oncorhynchus kisutch*) in Humboldt Bay, California

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Recent studies have shown the broad role estuaries plays in juvenile coho salmon (*Oncorhynchus kisutch*) life history; however, most of these studies were limited to the Pacific Northwest and did not include information from the southern end of its range in California. We sampled the stream-estuary ecotone (SEE) of numerous Humboldt Bay tributaries from 2003 to 2011 to document use by juvenile coho salmon. We sampled fish using seine nets and baited minnow traps and found that young-of-the-year (YOY) and yearling plus (1+) coho salmon reared primarily in freshwater or tidal freshwater habitat in the SEE. We detected three basic life history strategies employed by juvenile coho salmon regarding their use of the SEE. The first group were YOY fish that arrived in the spring and resided mostly in mainstem channel habitat in the summer and early fall; the second group of nearly 1+ fish arrived after the first large stream flow event in the fall and resided extensively in smaller tributary and off-channel habitat during the winter and spring; and finally a third group of stream-reared 1+ coho salmon emigrated through the SEE quickly during the following spring. Juvenile coho salmon resided in the SEE an average of one to two months but some individuals reared there for over a year. We found that about 40% of the coho salmon smolt production from Freshwater Creek, Humboldt Bay's largest tributary, originated from the SEE. Juvenile coho salmon rearing in the SEE were larger than their cohorts rearing in stream habitat upstream of the SEE. Our results demonstrate that juvenile coho salmon utilize portions of the Humboldt Bay SEE in ways similar to those reported in Pacific Northwest estuaries, and suggest that the SEE of Humboldt Bay provides quality rearing habitat—especially over winter rearing habitat—for those juveniles. By incorporating this knowledge into habitat restoration plans we can design effective habitat restoration projects to improve habitat conditions and non-natal rearing for juvenile coho salmon.

Key words: coho salmon, estuaries, Humboldt Bay, *Oncorhynchus kisutch*, over winter rearing habitat

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Estuaries have long been known as important habitat for juvenile Chinook salmon (*Oncorhynchus tshawytscha)* (Reimers 1971, Healey 1982, Kjelson et al.1982, Simenstad et al. 1982, Healey 1991) and coastal cutthroat trout (*Oncorhynchus clarki clarki*) (Northcote 1997, Trotter 1997) but until recently have not been thought to be important to coho salmon (*Oncorhynchus kisutch*). Though coho salmon were shown to use estuarine habitat in limited geographic areas (Tschaplinski 1982), the traditional model of their life cycle was that juveniles were born and resided in freshwater for a year or more, migrated quickly through the estuary to the sea as smolts, reared there for 18 months or more, and then returned to their stream of origin as adults to spawn and die (Sandercock 1991). Recently biologists have begun to appreciate the broader role that estuarine habitat plays among juvenile coho salmon over much of their range (Miller and Sadro 2003, Koski 2009, Craig 2010, Jones et al. 2014). However, estuarine habitat use by coho salmon has not been described at the southern end of their range in California where the species is listed as threatened under both state and federal endangered species acts (Federal Register 1997, CDFG 2002).

Simenstad et al. (1982) hypothesized that estuaries provided an advantage to rearing juvenile salmonids by providing a productive foraging area, refuge from predators, and an area to gradually shift from freshwater to marine habitats. For salmonids other than coho salmon, faster growth in the estuary and larger size at ocean entrance has been shown to account for increased marine survival (Nicholas and Hankin 1989, Northcote 1997, Pearcy 1997, Trotter 1997, Bond et al. 2008). For example, California steelhead trout (*Oncorhynchus mykiss)* populations use estuarine habitats for months at a time primarily to acclimate, forage, and grow (Bond et al. 2008). Holtby et al. (1990) reported, however, that size at ocean entry can be particularly important for coho salmon during periods of low ocean productivity. Potential survival benefits to coho salmon have largely been inferred from these studies, but coho salmon have substantially different life histories and, therefore, estuary use patterns that potentially differ from those of other salmonid species.

Recent studies have identified the importance of the greater transition zone, or ecotone (Odum 1971), between fresh and brackish water to juvenile salmonids (Miller and Sadro 2003, Koski 2009, Jones et al. 2014). Miller and Sadro (2003) defined this stream-estuary ecotone (SEE), and we adapt their definitions, to include the area of low gradient stream extending from stream entrance to the wide valley floor, through the upper limit of tidal influence downstream to the area where the channel becomes bordered by tidal mudflats.

This definition of the SEE includes all side channels, off channel ponds, tidal channels, and fringing marsh habitats that are accessible to fish for at least some portion of the tidal cycle.

Habitat quality is best defined as the benefit to survival or reproduction that an organism receives from using the habitat (Rosenfeld et al. 2005), and is often evaluated relative to other potential or available habitats. Understanding of the quality of differing habitats and its relative abundance on the landscape is requisite for informed resource management and targeted restoration. This is especially true for the freshwater rearing phase of juvenile coho salmon, where rearing areas can be dynamic over both time and space within a watershed, and multiple life history pathways potentially contribute differentially to the reproductive population (Jones et al. 2014, Nordholm 2014).

Generally, to consider the Humboldt Bay SEE as relatively high quality habitat for coho salmon one or more of the following should be true: coho salmon have prolonged residence in the SEE; multiple life stages of coho salmon use the SEE; a substantial portion of the population uses the SEE; the SEE provides productive foraging, resulting in increased growth rates or larger size; and the SEE supports coho salmon during stressful periods (i.e., summer, periods of drought, or winter high flows. We provide information to infer relative habitat quality of the SEE in tributaries of the Humboldt Bay watershed by presenting information regarding juvenile coho salmon movement and residence times (Winker et al. 1995), size at time or individual growth (Holtby et al. 1990), and habitat use (Rosenfeld 2003), and comparing this to similar information from riverine habitats upstream of the SEE. The goal of this paper is to describe the use of portions of the Humboldt Bay SEE by coho salmon and to demonstrate their patterns of estuarine use are similar to other populations in the Pacific Northwest as described by other researchers such as Miller and Sadro (2003) and Koski (2009).

Materials and Methods

Study area.—Humboldt Bay is located 442 km north of San Francisco, California, and its watershed area is 578 km^2 (HBWAC 2005). The two largest tributaries entering Humboldt Bay are Freshwater Creek with a drainage area of 9,227 ha^2 and Elk River with a drainage area of 8,632 ha^2 (HBWAC 2005). Many smaller tributaries, sloughs, and tidal streams contribute to a complex and dynamic hydrological regime in drainages around the bay (Figure 1). We defined sloughs as bodies of water with very low flow velocities and very low gradients regardless of tidal influence. We also characterized areas that experience changes in tidal heights, but are upstream of the influence of saltwater, as tidal freshwater. Tide gates are common on tributaries and sloughs entering Humboldt Bay, with 79 identified from a recent U.S. Fish and Wildlife Service (USFWS 2007) inventory. The lower portions of most streams entering Humboldt Bay flow through agricultural lands (primarily cattle grazing) and are characterized by low gradient, tidal ranges of 2–3 m, limited riparian vegetation, and confinement within levees. Physical conditions in Humboldt Bay tributaries such as saltwater intrusion show a high degree of annual, seasonal, and daily variation due to changes in stream flow and tidal inundation. The lower 2–4 km of Freshwater Creek and Elk River sloughs experience fluctuations in tidal height up to 3 m, and brackish water (25–30 ppt) is usually present from late spring through the early fall. Water temperatures of 20–25° C occur during the summer in the lower portion of Freshwater Creek Slough due to water heating up while on the mudflats during low tides, and limited tidal circulation

(Wallace 2006, Wallace and Allen 2015).

The tidal freshwater portions of most of the tributaries have water temperatures <18° C, and are maintained within confined channels (some within levees) having dense stands of riparian vegetation dominated by willow (*Salix* sp.) and alder (*Alnus* sp.). Lack of water turbulence and wind mixing in the freshwater-saltwater interface zone commonly results in a stratified water column with freshwater near the surface overlaying a wedge of brackish water near the bottom (Wallace 2006, Wallace and Allen 2015). Freshwater Creek Slough and Elk River Slough contain tidal slough habitat as they near Humboldt Bay, non-tidal low gradient stream habitat flowing through broad valleys upstream of the estuaries and higher gradient streams in steep canyons in the upper part of the watersheds (Figures 1 and 2). In Freshwater Creek the upstream end of the SEE is near the Howard's Heights

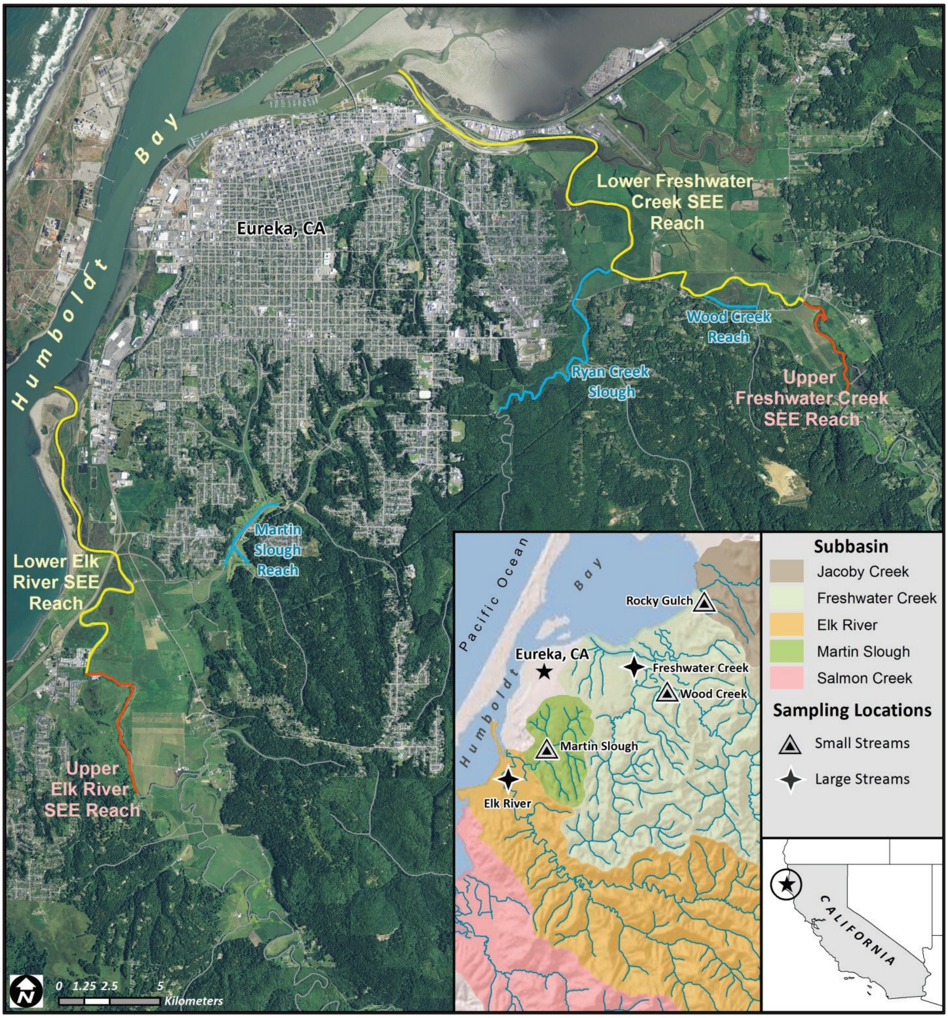

FIGURE 1.—Location of Humboldt Bay tributaries including demarcations of lower vs. upper sloughs in Freshwater Creek and Elk River along with Martin Slough and Wood Creek sampling areas Humboldt County, California. Lower and upper Freshwater Creek and Elk River sloughs are shown in yellow and red, respectively, and Martin Slough, Wood Creek, and Ryan Creek Slough are shown in blue.

downstream migrant trap (Figure 2). Smaller tributaries included in this study include Wood Creek, Martin Slough, and Rocky Gulch. These tributaries are within or proximal to Freshwater Creek, Elk River, and Jacoby Creek, respectively (Figures 1 and 2), which are the primary source populations of coho salmon in the Humboldt Bay watershed. Habitat conditions and land use of the small tributaries are similar to those described above. The largest tributary entering Freshwater Creek Slough is Ryan Creek (Figure 2). We did not sample this stream, but we did detect coho salmon tagged by Green Diamond Resources Company (described below) that emigrated from Ryan Creek into the lower Freshwater Creek watershed.

Seining and minnow trapping.—We sampled two large and three small Humboldt Bay tributaries, with a variety of gear, sampling frequencies, and time periods from 2003

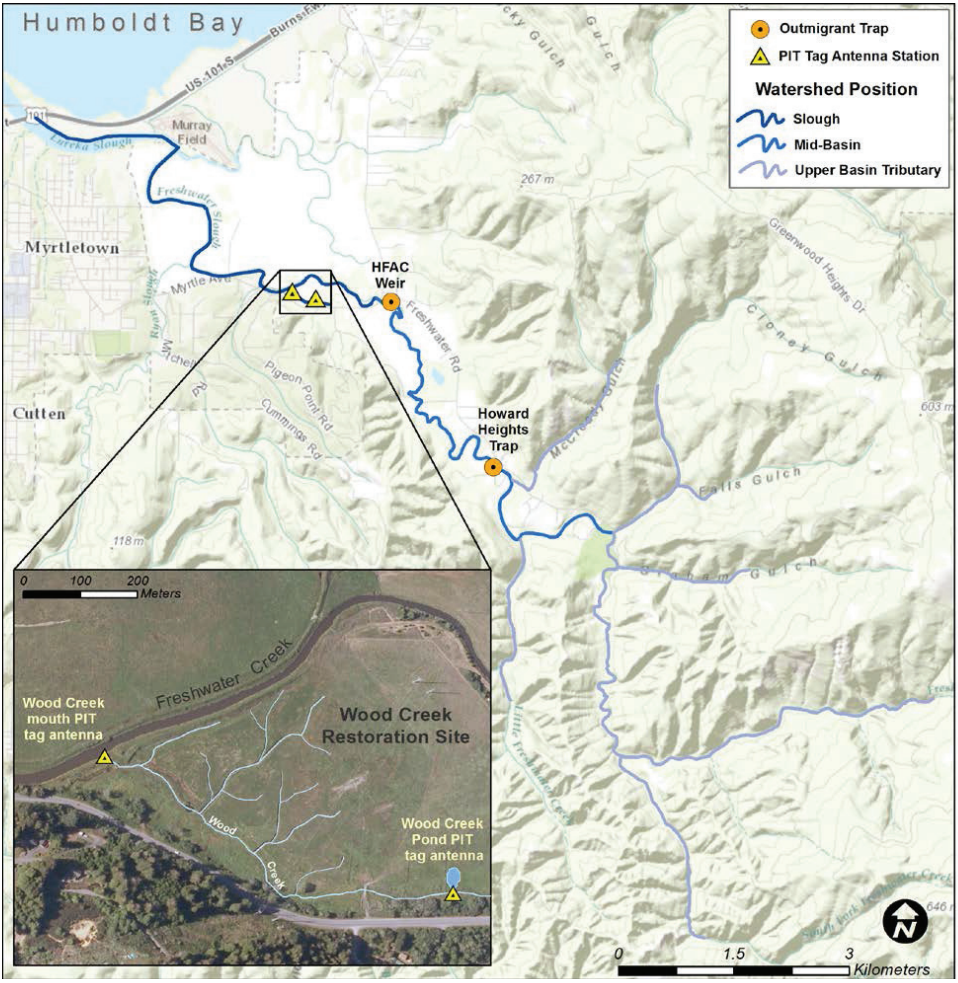

FIGURE 2.—Freshwater Creek basin showing locations of major tributaries, Howard Heights downstream migrant traps at the head of the broad valley floor, the Humboldt Fish Action Council (HFAC) fish trap in the stream-estuary ecotone, and PIT-tag antennas on Wood Creek, Humboldt County, California. Upstream extent of the SEE is located between Howard Heights Trap and McCready Gulch.

to 2011 (Table 1). In the slough portions of Freshwater Creek and Elk River we stratified sampling between the upper and lower sloughs due to differences in water salinity and the need to use different types of gear in the two sections of those sloughs. The stratification was necessary due to the presence of heavy riparian vegetation in the upper sloughs that required field crews to use a smaller seine net than that used to sample the larger water area in the lower sloughs. This is also the general area where riparian vegetation started to appear, representing a boundary between primarily estuarine and tidal freshwater habitat.

Table 1.—Sampling locations, methods, frequency, and duration conducted by this project in Humboldt Bay tributaries, Humboldt County, California, 2003–2011.

Location	Method	Frequency	Duration
Large streams			
Freshwater Creek			
upper	9-m seine	weekly	2003–2011
lower	30-m seine	weekly	2003–2009
Elk River			
upper	9-m seine	weekly	2005–2010
lower	30-m seine	weekly	2005–2010
Small streams			
Rocky Gulch	9-m seine; minnow trap	monthly	2007–2010
Wood Creek	minnow trap	monthly	2007–2011
Wood Cr. Pond	30-m seine	monthly	2009–2011
Martin Slough	9- & 30-m seines; minnow trap	monthly	2007–2010

We located sites to sample the slough continuum from the mouth to the upstream end of tidal influence. We chose individual seine sites based on the ability to pull a seine net through them and minnow trap sites in areas having perceived fish cover. We established six sampling sites in the upper slough of Freshwater Creek and four sites in upper Elk River Slough; those sloughs were 1.3 km and 1.7 km in length, respectively. Field crews made two hauls per sampling site using a 9.1 m × 1.8 m × 6.4-mm mesh beach seine. We established seven sampling sites in the lower slough of Freshwater Creek and five sites in lower Elk River Slough, and they were 8.5 km and 5.5 km in length respectively. Field crews made one seine haul per site using a 30.5 m × 2.4 m beach seine (mesh size of the wings was 19.1 mm and the bag was 1.5 m deep with 6.4-mm mesh) deployed by hand or boat. In the small tributaries we used a variety of sampling gear (Table 1). In Rocky Gulch, crews made two hauls at one site with the 9.1-m seine and deployed minnow traps baited with frozen salmon roe for 30 to 210 min at locations where seine hauls were precluded due to steep banks and heavy vegetation. In Wood Creek we deployed baited minnow traps for 30 to 210 min at sites. We made one to two hauls with the 30.5-m seine in a constructed pond connected to the Wood Creek channel. In Martin Slough we used the 30.5-m seine set by hand or kayak to sample a large pond, the 9.1-m seine to sample the slough channel, and baited minnow traps were deployed for 30 to 210 min where seine hauls were precluded due to steep banks and heavy vegetation.

Fish processing.—Field crews anaesthetized, identified, counted, and examined all juvenile coho salmon for marks and tags and determined life stage (i.e., parr, pre-smolt, smolt) of yearling plus (1+) coho salmon. We designated coho salmon as young-of-the-year (YOY) until the end of the calendar year after which we designated them as 1+. We distinguished 1+ from YOY coho salmon based on their greater fork length (FL). Crews measured FL to the nearest mm and weight to the nearest 0.1 g for all juvenile coho salmon except for the rare occasions when the number of fish captured (i.e., >100 fish/site) or environmental conditions, such as high water temperatures or high winds made it dangerous for the fish or for field crews to process the fish.

All fish with tags or marks were measured for FL, weighed, and their mark or tag number was recorded. We applied Passive Integrated Transponder (PIT) tags to untagged juvenile coho salmon by making a small incision along the ventral surface and inserting the tag into the body cavity. All coho salmon ≥70 mm FL received an 11.5 mm HDX PIT-tag. Starting in 2008, all coho salmon ≥55 mm and ≥69 mm FL received an 8.5 mm FDX PIT-tag. We also encountered and processed coho salmon containing PIT-tags applied by other fish monitoring projects in the Freshwater Creek basin (see below in *Data Analysis*). Once processed, the fish were allowed to fully recover for 10–30 min and then released at the sampling site.

Downstream migrant trapping.—In 2007 and 2008 we operated two downstream migrant traps on Freshwater Creek from early March to June to estimate coho salmon smolt production above each site and partition smolt production into that occurring above and between trap placements. The upstream trap was a floating inclined plane trap placed in the mainstem of Freshwater Creek 12.5 km upstream of the mouth where the stream exited steep canyons and entered low stream gradient habitat flowing through broad valley floor (Howards Heights Trap in Figure 2). The downstream trap was a modified adult salmon weir originally installed by the Humboldt Fish Action Council (HFAC) fitted with a pipe trap located in the lower coastal plain 8.5 km above the mouth (HFAC Weir in Figure 2). At this point the stream is usually freshwater but its elevation is strongly influenced by daily tidal cycles and brackish water extends up to this point at high tides during summer and early fall. Captured fish were processed with the same protocol as the SEE sampling, but all PIT-tagged fish were transported above the traps and released to help establish period-specific trap efficiency estimates that were used to expand total catch as an estimate of smolt production (Bjorkstedt 2005, Ricker and Andersen 2014).

PIT-tag antennas.—We installed two PIT-tag antenna arrays on Wood Creek, a small tributary entering Freshwater Creek Slough (Figure 2) to document the residence times and origin of PIT-tagged salmonids residing in, or passing by, Wood Creek. The first was placed at the entrance of the newly constructed off-channel pond on 29 January 2010 and the second was installed at the mouth of Wood Creek in the tide gate structure on 22 February 2010; both were operated throughout the length of this study. We installed two independent antennas at each site to discern directional movement in and out of the pond and creek. Each PIT-tag antenna array consisted of a multiplex transceiver (Mauro Engineering) and data logger powered by two 12V batteries that were continuously charged by a solar panel. Antennas were constructed of copper tubing and sealed inside PVC pipe. At the pond site we attached the two antennas to wooden posts driven into the substrate. At the tide gate site we attached wooden tracks to the concrete tide gate structure and slid the antennas into the tracks.

Data analysis.—To assess residency time and growth in the SEE, we included all fish marked either in the SEE, or upstream in the greater basin and later recaptured in the SEE (Figure 2). We calculated length of SEE residence for PIT-tagged fish by combining fish captures and antenna recordings to determine the number of days between tagging or first detection in the SEE and last recapture or detection date. Calculated growth rates were simply the change in FL between date of tagging or first capture and date of last recapture divided by the number of days at large between first and last encounter. Mean residence times were not calculated for YOY or 1+ coho salmon when sample sizes were composed of <10 individuals to limit the influence of the occasional individual exhibiting extreme residence time. Growth rates were not calculated for fish-at-large ≤12 days to minimize short-term tagging effects on growth rate calculations. The lower downstream migrant trap (HFAC Weir; Figure 2) was also operated as an adult salmonid counting weir by CDFW to obtain annual adult coho salmon run size estimates using mark-recapture techniques (Ricker and Anderson 2011).

We used analysis of variance (ANOVA) to investigate spatial and temporal differences in the mean fork length of coho salmon rearing in different portions of the SEE during the spring, and between the SEE and upper stream network during the fall. Residual plots and length-frequency histograms were examined to detect outliers and to test for violations of ANOVA assumptions (i.e., homoscedasticity and normality).

To analyze differences in 1+ coho salmon FLs in spring, we compared the data collected annually between March 1 and May 29 by basin (freshwater elk), year, and location (slough type) within the SEE. For the fall, we only analyzed Freshwater Creek YOY coho salmon length data because we did not collect any size data from fish upstream of the SEE in Elk River. Furthermore, we collected length data from YOY coho salmon rearing in upper Freshwater Creek basin streams, and in the mid-basin upstream of the SEE, allowing us to compare mean fall fork length throughout the entire stream network from the SEE to headwater reaches. To analyze differences in YOY coho salmon FLs in fall, we compared the data collected annually between September 9 and November 11 by basin, year, and location within SEE. Significance levels were set at $P<0.05$ and all post-hoc comparisons of groups were performed using Tukey-Kramer multiple comparisons (Zar 1999).

Results

Juvenile coho salmon were widely distributed throughout the sampled portion of the Humboldt Bay SEE. Catches of juvenile coho salmon varied between years and life stage in upper Elk River and Freshwater Creek sloughs (Figure 3). Young-of-the-year coho salmon were present in these large tributaries from roughly April to December with peak catches in June and July, while 1+ coho salmon were present mostly January to June with peak catches in April and May (Figure 3). In upper Freshwater Creek Slough, where we had the longest time series, we used our June catch-per-unit-effort (CPUE) of YOY coho salmon as an index of relative abundance between years and detected large variations in their annual abundance in the SEE (Table 2). We also found that June CPUE of YOY coho salmon was positively correlated ($r^2 = 0.87$) with adult coho salmon escapement from the previous winter (Figure 4).

Seasonality of peak juvenile coho salmon catches also varied between tributary size and life stage. In the larger tributaries, YOY coho salmon comprised a majority of the catches and usually peaked in spring and summer (Table 3) while in small tributaries catches of primarily 1+ coho salmon peaked in the winter when stream flows were high (Table 4). Conversely, the lowest seasonal catches of coho salmon in large streams usually occurred in the winter while the lowest catches of coho salmon in small streams occurred primarily in the summer and fall (Tables 3 and 4). This resulted in a dyssynchronous seasonal pattern of juvenile coho salmon occupation between large and small tributaries (Figure 5).

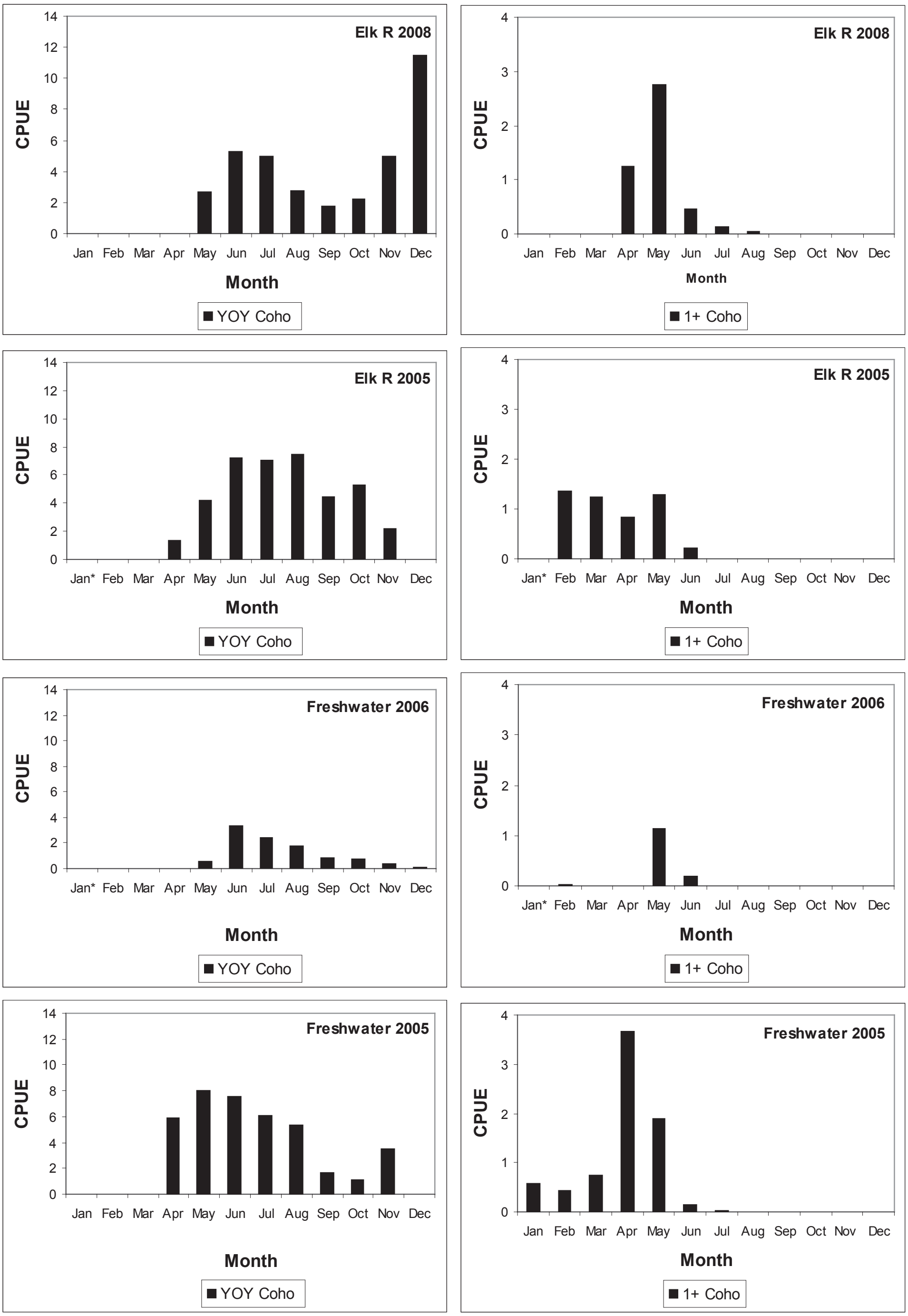

FIGURE 3.—Catch-per-unit-effort (# of fish/seine haul) of young-of-the-year (YOY) and yearling plus (1+) coho salmon from upper Freshwater Creek and Elk River sloughs, Humboldt County, California, for selected years.

Table 2.—Effort, number captured, and catch-per-unit-effort (CPUE) of young-of-the-year coho salmon in upper Freshwater Creek Slough, Humboldt County, California, during the month of June, 2003–2011.

Year	Seine Hauls (*n*)	Fish Caught (*n*)	CPUE (fish/haul)
2003	48	478	9.96
2004	60	335	5.58
2005	59	447	7.58
2006	48	161	3.35
2007	48	64	1.33
2008	44	4	0.09
2009	34	106	3.34
2010	10	2	0.20
2011	24	33	1.38

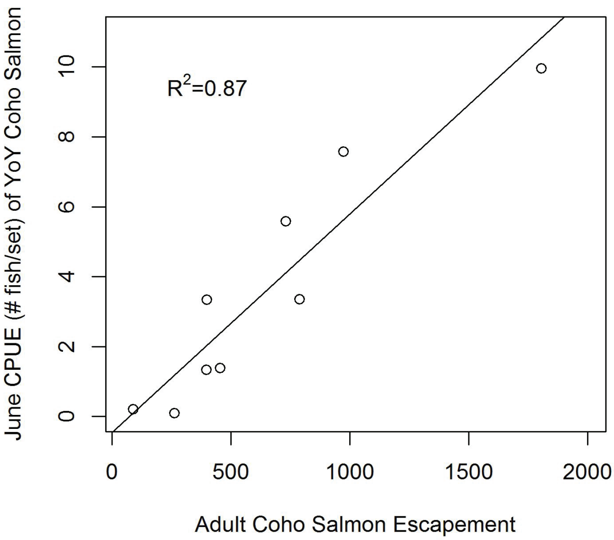

Figure 4.—Relationship between adult coho salmon escapement and subsequent catch-per-unit-effort (CPUE) of young-of-the-year (YOY) coho salmon progeny captured in upper Freshwater Creek Slough, Humboldt County, California, the following June.

Table 3.—Catch-per-unit-effort of young-of-the-year (YOY) and yearling plus (1+) coho salmon captured in Freshwater Creek Slough and Elk River Slough, Humboldt County, California, by season, 2007–2010. Winter is January to March, Spring is April to June, Summer is July to September, and Fall is October to December.

	Freshwater Creek Slough		Elk River Slough		Combined Sloughs	
Season	1+	YOY	1+	YOY	1+	YOY
Winter 2007	0.20	0.00	0.00	0.00	0.14	0.00
Spring 2007	1.44	0.92	1.19	2.35	1.35	1.43
Summer 2007	0.01	0.37	0.03	2.97	0.02	1.39
Fall 2007	0.00	0.38	0.00	1.18	0.00	0.70
Winter 2008	0.00	0.00	0.00	0.00	0.00	0.00
Spring 2008	0.27	0.06	1.36	2.43	0.75	1.10
Summer 2008	0.03	0.04	0.07	3.50	0.04	1.39
Fall 2008	0.00	0.02	0.00	4.31	0.00	1.53
Winter 2009	0.04	0.00	0.64	0.00	0.30	0.00
Spring 2009	0.36	1.57	5.02	3.18	2.31	2.24

Table 4.—Number of young-of-the-year (YOY) and yearling plus (1+) coho salmon captured in Wood Creek, Martin Slough, and Rocky Gulch, Humboldt County, California, by season, 2007–2010. Winter is January to March, Spring is April to June, Summer is July to September, and Fall is October to December.

	Wood Creek		Martin Slough		Rocky Gulch		Combined	
Season	1+	YOY	1+	YOY	1+	YOY	1+	YOY
Winter 2007	86	0	4	0	68	0	158	0
Spring 2007	27	2	71	0	33	1	131	3
Summer 2007	1	16	0	17	0	0	1	33
Fall 2007	0	17	0	24	0	1	0	42
Winter 2008	125	0	68	0	20	0	213	0
Spring 2008	50	0	70	0	16	0	136	0
Summer 2008	0	1	0	13	0	0	0	14
Fall 2008	1	4	0	37	0	0	1	41
Winter 2009	46	0	435	0	28	0	509	0
Spring 2009	19	3	246	1	3	0	268	4
Summer 2009	1	3	17	31	0	0	18	34
Fall 2009	1	3	8	8	0	1	9	12
Winter 2010	140	0	198	0	76	0	414	0
Spring 2010	19	3	83	0	38	0	140	3

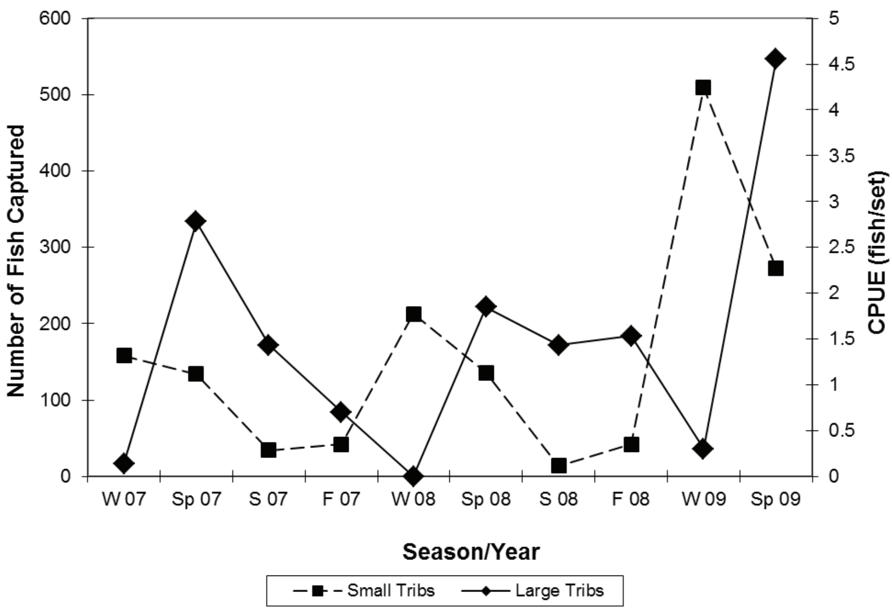

Figure 5.—Comparison of the number of yearling plus (1+) and young-of-the-year (YOY) coho salmon captured in minnow traps by season in Rocky Gulch, Wood Creek, and Martin Slough (small tributaries) and combined catch-per-unit-effort (CPUE) of 1+ and YOY coho salmon captured by seining in upper Freshwater Creek and Elk River sloughs (large tributaries), Humboldt County, California, 2007–2009. W= winter, Sp= spring, S= summer, and F= fall.

Both YOY and 1+ coho salmon reared for extended periods in the sampled portions of the Humboldt Bay SEE. YOY coho salmon resided primarily in the upper sloughs of the larger streams during the spring and summer. The mean residence times of PIT-tagged YOY coho salmon that were tagged and recaptured as YOY ranged from one to two months, but individual fish reared for up to six months (Table 5); some individual fish tagged as YOY

Table 5.—Summary of residence times in days at liberty (DAL) and growth rates (GR) in mm/day of young-of-the-year coho salmon in Freshwater Creek Slough, Elk River Slough, Martin Slough, Wood Creek, Rocky Gulch, and Ryan Creek, Humboldt County, California, 2005–2010. Mean days at liberty were not calculated for fish with sample sizes less than 10 individuals and mean growth rates were not calculated for fish at large ≤12 days except where noted.

Basin	Year	*n*	Mean DAL	Range DAL	Mean GR	Range GR
Freshwater	2010	12	41	16-113	0.23	0.12-0.48
	2009	69	60	13-175	0.20	0.00-0.68
	2008	0	-	-	-	-
	2007	12	68	6-167	0.17	0.12-0.45
	2006	57	33	5-106	0.15	0.00-0.29
	2005	112	32	4-128	0.17	0.00-0.43
Elk	2009	19	17	13-27	0.46	0.31-0.64
	2008	104	58	6-168	0.29	0.04-0.68
	2007	55	44	5-124	0.16	0.00-0.38
	2006	41	39	6-128	0.19	0.07-0.39
	2005	121	34	4-110	0.13	0.00-0.38
Martin	2010	0	-	-	-	-
	2009	4	-	28-126	-	0.21-0.43
	2008	0	-	-	-	-
	2007	4	-	30-58	-	0.27-0.33
Wood	2010	1	-	29	-	0.14
	2009	1	-	58	-	0.17
	2008	0	-	-	-	-
	2007	4	-	26-129	-	0.03-0.22
Rocky	2010	0	-	-	-	-
Gulch	2009	0	-	-	-	-
	2008	0	-	-	-	-
	2007	0	-	-	-	-
Ryan	2010	0	-	-	-	-

and recaptured as 1+ reared in the SEE for over a year (Table 6). The 1+ coho salmon reared mostly during the winter in both the larger and smaller streams and the mean residence times of PIT-tagged 1+ coho salmon ranged from a few weeks to nine months (Table 6). In the more brackish, lower sloughs of Freshwater Creek and Elk River, the presence of YOY and 1+ coho salmon was confined mostly to spring (Wallace 2006, Wallace and Allen 2009, Wallace and Allen 2012).

Young-of-the-year coho salmon were captured only in the lower sloughs during spring freshets and did not rear extensively in lower Freshwater Creek Slough but some did move into Wood Creek, which enters Freshwater Creek in the lower slough. Coho salmon categorized as 1+ were consistently captured in the lower sloughs from April to June. The residence times of 1+ coho salmon in the lower sloughs were much shorter than in the areas upstream of brackish water, but some fish were found to rear for one to four weeks in lower Freshwater Creek Slough (Wallace 2006; Wallace and Allen 2009, 2012; Pinnix et al. 2012).

Table 6.— Summary of residence times in days at liberty (DAL) and growth rates (GR) in mm/day of yearling 1+ coho salmon in Freshwater Creek Slough, Elk River Slough, Martin Slough, Wood Creek, Rocky Gulch, and Ryan Creek, Humboldt County, California, 2005–2010. Mean days at liberty were not calculated for fish species or life stage with sample sizes less than 10 individuals and mean growth rates were not calculated for fish at large ≤12 days except where noted. The table also includes fish tagged as young-of-the-year (YOY) and recaptured the following year.

Basin	Year	*n*	Mean DAL	Range DAL	Mean GR	Range GR
Freshwater	2010	0	-	-	-	-
	2009	1	-	-	-	-
	2008	1	-	-	-	-
	2007	22	21	5-224	0.43	0.23-0.60
	2006	4	-	5-11	-	-
	2005	20	20	2-81	0.42	0.21-0.56
	Tagged YOY	2	-	170-245	-	0.15-0.17
Elk	2009	18	19	13-42	0.30	0.00-0.54
	Tagged YOY	5	-	133-349	-	0.14-0.18
	2008	19	14	5-25	0.37	0.17-0.72
	Tagged YOY	1	-	294	-	0.10
	2007	8	-	7-258	-	0.09-0.50
	2006	7	-	6-282	-	0.18
	2005	3	-	9-94	-	0.11-0.33
Martin	2010	17	50	27-119	0.41	0.21-0.76
	Tagged YOY	3	-	64-310	-	0.14-0.25
	2009	33	42	23-126	0.32	-0.04-0.67
	Tagged YOY	5	-	67-270	-	0.13-0.20
	2008	14	34	25-60	0.32	0.16-0.51
	2007	1	-	39	-	1.03
Wood	2010	6	-	9-153	-	0.11-0.73
	2009	5	-	23-91	-	0.03-0.35
	2008	7	-	28-57	-	0.05-0.32
	Tagged YOY	3	-	110-449	-	0.10-0.17
	2007	5	-	35-70	-	0.13-0.43
	Tagged YOY	2	-	213-251	-	0.12-0.12
Rocky Gulch	2010	13	43	28-94	0.33	0.12-0.45
	Tagged YOY	1	-	90	-	0.21
	2009	4	-	43-69	-	0.09-0.26
	2008	2	-	30-30	-	0.10-0.13
	2007	6	-	10-37	-	0.27-0.41
Ryan	2010	22	49	14-90	0.46	0.20-0.75

Typically, in the upper sloughs of Freshwater Creek and Elk River the monthly mean FL of captured YOY coho salmon increased from around 40 mm in early spring to 80–110 mm by the end of the year (Table 7). The mean monthly FL of 1+ coho salmon captured in the upper sloughs was typically around 80 mm in the winter and increased to 105–115 mm during April and May (Table 7). The monthly mean FL of the small numbers of YOY coho salmon in the lower sloughs was around 40 mm in early spring and 65–85 mm by the end of the year (Table 8). The mean monthly FL of 1+ coho salmon captured in the lower slough was typically 65–80 mm in the winter and increased to 110–120 mm during the spring and early summer (Table 8).

Yearling (1+) coho salmon captured in the lower sloughs of Freshwater Creek and Elk River were significantly larger (mean FL = 114 mm, SE = 0.54 mm) than those captured in the upper sloughs (mean FL = 106 mm, SE = 0.41 mm); ANOVA, $F_{1,1479} = 90.86$, $P<0.001$

TABLE 7.—Monthly mean fork length (FL) and size range in millimeters of young-of-the-year (YOY) and yearling plus (1+) coho salmon in upper Freshwater Creek Slough and upper Elk River Slough, Humboldt County, California, for selected years.

Freshwater Creek Slough												
	2005				2007				2009			
	YOY Coho		1+ Coho		YOY Coho		1+ Coho		YOY Coho		1+ Coho	
Month	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range
Jan	-	-	77	64-86	-	-	-	-	-	-	-	-
Feb	-	-	80	70-100	-	-	-	-	-	-	-	-
Mar	-	-	81	67-96	-	-	83	67-100	-	-	-	-
Apr	40	33-50	104	81-133	42	34-47	100	85-134	34	34-34	110	90-127
May	43	31-61	102	79-123	54	39-67	100	76-127	42	35-48	106	93-114
Jun	57	29-96	106	92-136	65	31-75	101	82-111	64	40-85	106	100-110
Jul	66	51-99	98	98	79	69-91	123	123	77	66-90	-	-
Aug	73	56-93	-	-	86	80-97	-	-	80	63-94	106	96-115
Sep	77	59-95	-	-	88	85-94	-	-	83	71-95	-	-
Oct	82	70-101	-	-	86	63-105	-	-	87	70-99	-	-
Nov	79	57-113	-	-	85	76-101	-	-	90	70-103	-	-
Dec	-	-	-	-	-	-	-	-	-	-	-	-

Elk River Slough												
	2005				2007				2008			
	YOY Coho		1+ Coho		YOY Coho		1+ Coho		YOY Coho		1+ Coho	
Month	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range
Jan	-	-	-	-	-	-	-	-	-	-	-	-
Feb	-	-	80	64-100	-	-	-	-	-	-	-	-
Mar	-	-	82	62-93	-	-	-	-	-	-	-	-
Apr	41	37-53	113	98-129	-	-	-	-	39	39	111	80-125
May	41	35-67	114	97-142	54	34-70	109	80-139	53	39-63	107	87-125
Jun	59	43-81	107	88-119	62	45-82	104	86-125	63	45-79	106	94-116
Jul	68	51-90	-	-	73	52-95	105	100-114	74	58-97	118	101-141
Aug	71	57-94	-	-	80	65-100	-	-	84	67-102	118	118
Sep	75	63-95	-	-	90	84-97	-	-	90	74-101	-	-
Oct	80	67-97	-	-	86	54-97	-	-	94	76-111	-	-
Nov	78	60-93	-	-	78	58-100	-	-	96	86-112	-	-
Dec	-	-	-	-	-	-	-	-	111	80-124	-	-

(Figure 6). No interactions were found between basin and slough type, indicating the lower sloughs of both basins contained larger yearling coho salmon; ANOVA, $F_{1,1474} = 1.05$, $P = 0.31$. Overall, year had a significant effect on mean yearling coho salmon FLs for both basins; Tukey post-hoc comparisons indicated the 2005 coho salmon were much smaller and the 2006 coho salmon were much larger than those measured from 2007 to 2009; ANOVA, $F_{4,1480} = 38.00$, $P<0.001$ (Figure 6). However, the interaction between year and slough type on mean coho salmon FLs was not significant, indicating mean FLs were consistently larger in lower sloughs regardless of their annual size or basin of origin; ANOVA, $F_{4,1470} = 1.47$, $P = 0.21$. The interaction of year and basin was significant indicating annual differences in mean coho salmon FLs were largely basin-specific instead of a regional trend; ANOVA, $F_{4,1475} = 10.49$, $P<0.001$. Last, yearling coho salmon captured during the spring from 2005 to 2009 were slightly larger on average in Elk River (mean FL = 111 mm, SE = 0.44 mm) than in Freshwater Creek (mean FL = 105 mm, SE = 0.62 mm); ANOVA, $F_{1,1484} = 12.12$, $P<0.001$; the 6-mm size difference is, however, unlikely to be biologically meaningful.

Young-of-the-year coho salmon in the Freshwater Creek SEE were larger than their cohorts rearing upstream and their FLs increased from the upper tributaries to the mid-basin to the SEE (Figure 7). Young-of-the-year coho salmon captured in Freshwater Creek during the fall of 2009 and 2010 were significantly larger in the mid-basin than those captured in upper tributaries; ANOVA, $F_{2,2218} = 97.94$, $P <0.001$. Mean FLs were 87 mm (SE = 0.67

Table 8.—Monthly mean fork length (FL) and size range in millimeters of young-of-the-year (YOY) and yearling plus (1+) coho salmon in lower Freshwater Creek Slough and lower Elk River Slough, Humboldt County, California, for selected years.

	Freshwater Creek Slough											
	2005				2007				2008			
	YOY Coho		1+ Coho		YOY Coho		1+ Coho		YOY Coho		1+ Coho	
Month	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range
Jan	-	-	-	-	-	-	-	-	-	-	-	-
Feb	-	-	-	-	-	-	-	-	-	-	-	-
Mar	39	39	83	62-127	-	-	-	-	-	-	-	-
Apr	39	33-45	113	86-125	-	-	105	83-151	-	-	113	105-127
May	49	32-60	117	90-146	42	42	107	95-118	-	-	114	101-124
Jun	65	60-70	104	94-112	-	-	-	-	-	-	122	122
Jul	-	-	-	-	-	-	-	-	-	-	94	94
Aug	76	74-78	-	-	-	-	-	-	-	-	-	-
Sep	80	77-83	-	-	-	-	-	-	-	-	-	-
Oct	-	-	-	-	-	-	-	-	-	-	-	-
Nov	77	62-94	-	-	-	-	-	-	-	-	-	-
Dec	-	-	-	-	-	-	-	-	-	-	-	-

	Elk River Slough											
	2005				2007				2008			
	YOY Coho		1+ Coho		YOY Coho		1+ Coho		YOY Coho		1+ Coho	
Month	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range	Mean FL	Range
Jan	-	-	64	60-68	-	-	-	-	-	-	72	55-89
Feb	-	-	82	60-105	-	-	-	-	-	-	-	-
Mar	39	39	90	76-117	-	-	113	108-119	-	-	-	-
Apr	41	35-46	110	73-136	-	-	127	109-139	-	-	119	94-143
May	47	37-71	107	74-133	42	42	119	91-183	-	-	109	90-133
Jun	64	62-69	110	95-126	-	-	109	86-125	-	-	120	101-143
Jul	-	-	129	129	-	-	-	-	-	-	128	111-141
Aug	-	-	-	-	-	-	-	-	-	-	-	-
Sep	87	86-87	-	-	-	-	-	-	-	-	-	-
Oct	-	-	-	-	-	-	-	-	-	-	-	-
Nov	-	-	-	-	-	-	-	-	-	-	-	-
Dec	66	61-70	-	-	-	-	-	-	-	-	-	-

mm) for the slough (SEE) locations, 80 mm (SE = 0.46 mm) for the mid-basin locations, and 72 mm (SE = 0.32 mm) for the upper tributary locations. Also, overall FLs of YOY coho salmon rearing throughout Freshwater Creek were substantially larger in 2010 (2010 mean FL = 79 mm, SE = 0.31 mm) than in 2009 (2009 mean FL = 71, SE = 0.45 mm); ANOVA, $F_{1,2217}$ = 1255.11, P<0.001 (Figure 7). No interaction was detected between watershed position and year, indicating mean FLs were progressively larger in the lower watershed than in the upper watershed regardless year (Figure 7); ANOVA, $F_{2,2215}$ = 0.77, P <0.001).

Annual mean growth rates of PIT-tagged YOY coho salmon rearing in the SEE ranged from 0.13 to 0.46 mm/day, but individual fish grew up to 0.68 mm/day (Table 5). Annual mean growth rates of PIT tagged 1+ coho salmon ranged from 0.30 to 0.46 mm/day, but individual fish grew up to 1.03 mm/day (Table 6).

The PIT-tag antennas at Wood Creek detected PIT-tagged juvenile coho salmon originally tagged throughout the Freshwater Creek watershed; in some cases those fish were from many kilometers upstream (Table 9). The antennas detected juvenile salmonids moving into Wood Creek and the pond to rear over winter during high stream flows. The pond PIT-tag antenna detected 46 coho salmon originally tagged by CDFW personnel in and upstream of the SEE in 2010, and 28 in 2010–2011 (Table 9).

A large portion of coho salmon smolt production uses the Freshwater Creek SEE. California Department of Fish and Wildlife calculated smolt production estimates entering

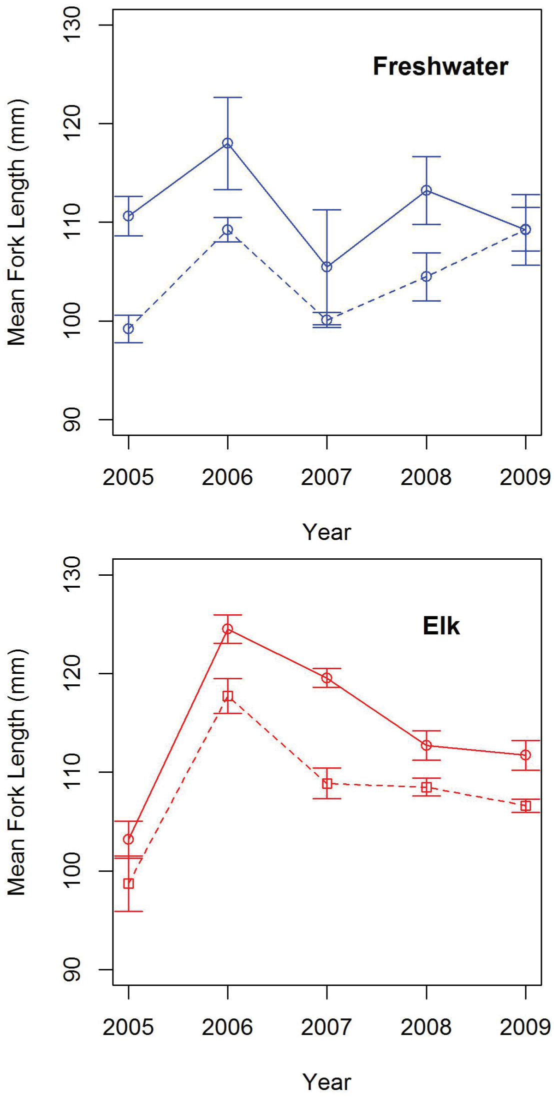

Figure 6.—Comparison of the annual mean fork lengths and standard errors of age 1+ coho salmon from upper Freshwater Creek and Elk River sloughs (dotted lines) and lower Freshwater Creek and Elk River sloughs (solid lines), Humboldt County, California, 2005–2009.

the SEE and within the SEE in 2007 and 2008. The 2007 coho salmon smolt estimates were 3,685 ± 266 at the Howards Heights Trap at the upstream end of the SEE (Figure 2) and 5,888 ± 503 at the HFAC Weir within the SEE. In 2008, the coho salmon smolt estimates were 3,096 ± 154 at the Howard Heights Trap and 4,945 ± 232 at the HFAC Weir (Ricker and Anderson 2011). These smolt estimates indicate ~40% of the coho smolt production in these two years were already present in this 4-km section of the SEE compared to ~60% residing in the 21 km of coho salmon habitat upstream of the Howard Heights Trap.

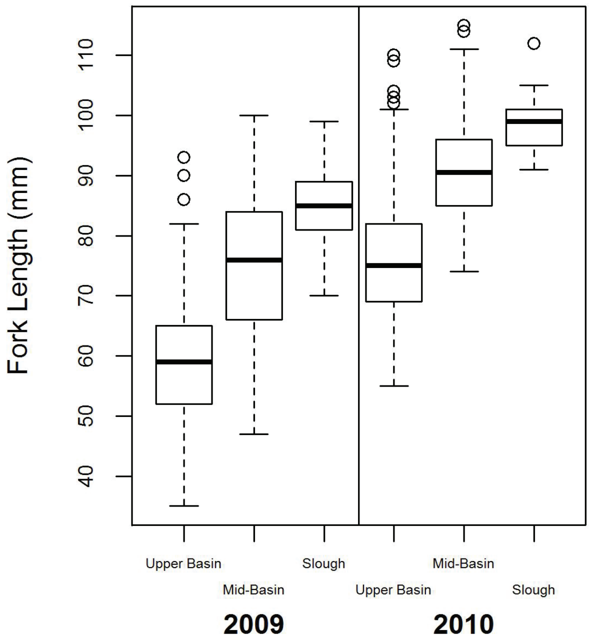

FIGURE 7.—Box plots comparing mean fork lengths of young-of-the-year coho salmon captured in the slough (stream-estuary ecotone), mid-basin, and upper basin portions of Freshwater Creek, Humboldt County, California, in the fall of 2009 and 2010. Boxes depict the 25th, 50th, and 75th percentiles, whiskers depict 5th and 95th percentiles, and points indicate outliers.

TABLE 9.—Origin of PIT-tagged juvenile coho salmon tagged in Freshwater Creek basin, Humboldt County, California, detected at Wood Creek pond and tide gate antennas during January to September 2010 and during October 2010 to June 2011.

Fish Origin	Pond 2010	Pond 2010/11	Tide Gate 2010	Tide Gate 2010/11
Stream-Estuary Ecotone	7	1	9	30
Lower Mainstem	11	6	11	49
Middle Mainstem	-	11	-	79
Upper Mainstem	7	6	10	59
Little Freshwater Cr	12	-	13	-
Cloney Gulch	9	4	8	45
South Fork Freshwater Cr	-	0	-	13
Freshwater Creek (total)	46	28	51	275
Wood Cr Pond	74	8	33	2
Wood Cr (tagged 2011)	-	6	-	17
Wood Cr (tagged 2010)	26	3	47	5
Wood Cr (tagged 2009)	1	0	1	0
Ryan Sl/Cr	0	0	26	5
Freshwater Sl (tagged 2011)	-	0	-	2
Freshwater Sl (tagged 2010)	0	0	2	8
Freshwater Sl (tagged 2009)	5	0	9	0
HFAC Weir (tagged 2011)	-	0	-	122
HFAC Weir (tagged 2010)	0	0	161	1
HFAC Weir (tagged 2009)	1	0	1	0
Grand Total	153	45	331	437

Discussion

Craig (2010) provided an excellent description of the various coho salmon life history patterns, moving from the traditional almost exclusively “stream-type” life history pattern (Sandercock 1991) to appreciating the multiple life history patterns exhibited by coho salmon where the SEE plays an important role in their development. These diverse patterns include, but are not limited to arriving and rearing in the SEE during spring and summer as fry (Miller and Sadro 2003, Wallace 2006, Jones et al. 2014); coho salmon parr arriving in the fall to rear during winter in the SEE (Koski 2009, Jones et al. 2014), or even moving into the marine environment as YOY fish (Bennett et al. 2015). Rearing fry and parr may over winter in the SEE or move into adjacent non-natal streams (Craig 2010, Jones et al. 2014, this study) or exhibit the “nomad” life history of moving back upstream to overwinter (Miller and Sadro 2003, Koski 2009).

A review by Koski (2009) showed juvenile coho salmon rear in the SEE from southwestern Alaska to southern Oregon. The redistribution and use of non-natal streams by juvenile coho salmon has been briefly noted in California streams including the Smith River (Parish and Garwood 2015), Klamath River (YTFP 2009), Redwood Creek (Bob Pagliuco, NOAA Restoration Center, personal communication November 2014), Eel River (Renger and Blessing 2014), and Russian River (SCR 2014). Our results indicate this life history strategy is prominent in multiple tributaries entering Humboldt Bay, California (Figure 8).

The SEE around Humboldt Bay appears to meet criteria for classification as relatively high quality habitat for juvenile coho salmon as outlined in the introduction. We found that the SEE (1) provided non-natal rearing habitat for prolonged residence by juvenile coho salmon (Tables 5 and 6); (2) supported multiple life stages (i.e. summer YOY and winter 1+) of coho salmon; (3) supported a substantial portion (~40%) of the coho salmon smolt population from throughout the basin (Table 9); (4) allowed juvenile coho salmon to obtain a larger size (Figures 6 and 7), and presumably grow faster than their stream dwelling conspecifics; and (5) provided slow-water habitat that appears to be limited in the upper stream channels during a stressful period due to high winter stream flows.

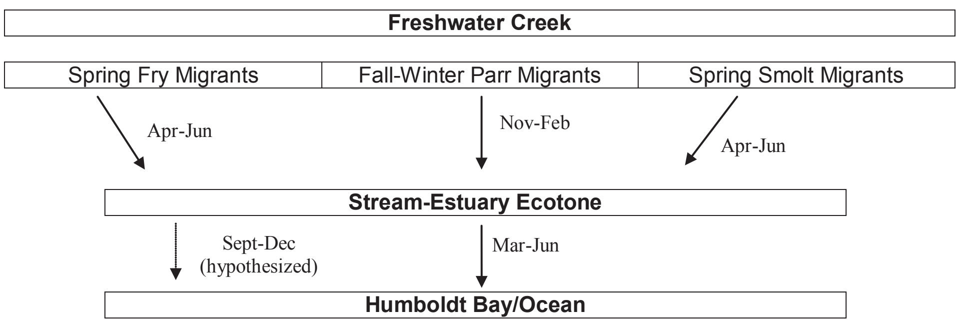

Figure 8.—Diagram of juvenile coho salmon life history pattern in Freshwater Creek watershed, Humboldt County, California (modified from Craig 2010).

Young-of-the year coho salmon moved to the SEE of Freshwater Creek and Elk River during spring and resided there throughout the summer. This pattern is similar to that observed in other Pacific Northwest estuaries (Tschaplinski 1987, Miller and Sadro 2003, Koski 2009). We do not know the underlying cause of this movement, but other researchers have suggested density dependent factors upstream (Chapman 1962, Hartman et al. 1982), high flushing stream flows (Tschaplinski 1987), or expressions of genotypic or phenotypic variation (Healey 2009, Waples et al. 2009). Regardless of the reasons for their movement into the SEE, once there coho salmon resided almost exclusively in the freshwater portion of the SEE. Furthermore, based on our PIT-tag data, most YOY coho salmon moved very little during the summer, with >90% of recaptured fish being caught at the same location at which they had been marked (Wallace and Allen 2007, 2009, 2012). Similar individual site fidelity has also been documented in studies in other Pacific Northwest estuaries (Tschaplinski 1987, Miller and Sadro 2003).

We found tidal and salinity influences on the SEE were most dynamic during the summer and we often observed coho salmon residing in the surface freshwater layer when the water column is stratified and the more dense brackish water is present along the bottom. Coho salmon residing here were more silvery in appearance and had much less pronounced parr marks than their conspecifics upstream in typical stream habitat, indicating they may occasionally be exposed to salt water. Later in the summer and early fall we captured small numbers of YOY coho salmon in brackish water. These fish were >70 mm FL and may have reached a size adequate to be able to adapt to saltwater. Other investigators have shown that salinity tolerances were a function of size, rather than age, in coho salmon (Conte et al. 1966; Weisbart 1968 as cited by Koski 2009). Other investigators documented sub-yearling coho salmon enter the marine environment, survive, and return as spawning adults, especially when they are ≥70 mm FL (Bennett et al. 2015). Most YOY coho salmon rearing in the Humboldt Bay SEE were ≥70 mm FL by the end of their first summer, and some may take on the sub-yearling ocean entry life history.

Abundance of YOY coho salmon usually peaked in Freshwater Creek and Elk River sloughs during June and July and then declined to low levels in late summer and early fall (Figure 3), likely as a result of mortality and seasonal movement in the SEE. During the subsequent winter and spring we recaptured fish tagged the previous summer in the vicinity of where they were originally marked or further downstream in tidal tributaries including Wood Creek in the Freshwater Creek watershed and Martin Slough in the Elk River watershed. Although we did detect juvenile coho salmon moving upstream in tributaries entering the SEE, we never detected any substantial upstream movement in the main stem of Freshwater Creek and Elk River sloughs. For example, during the six years of operation we never captured a fish tagged in the SEE at the Howard Heights Trap (approximately 4 km upstream of our SEE sample sites). Therefore, it appears that YOY coho salmon that rear in the sampled portion of the Humboldt Bay SEE during the summer stay in place, have a net downstream movement to over winter in lower mainstem portion or small tributaries of the SEE, perish, or enter the ocean as sub-yearling fish. Other than moving back upstream to over winter, these life history patterns are similar to those reported in Pacific Northwest estuaries (Miller and Sadro 2003, Koski 2009, Jones et al. 2014).

Coho salmon moved from stream habitat downstream to the SEE of Freshwater Creek during the first large stream flows in the fall and winter. Relatively large numbers of 1+ coho salmon moved into small and low gradient non-natal tributaries surrounding Humboldt Bay such as Martin Slough, Wood Creek, and Rocky Gulch (Table 4). These small tributaries were generally unsuitable for juveniles during summer and fall due to high water temperature and salinity, but provided good over winter rearing habitat with refuge from high stream flows. In Freshwater Creek our PIT-tag antennas documented movement of PIT-tagged juvenile coho salmon from throughout the watershed and downstream to

Wood Creek (Table 9). Rebenack et al. (2014) estimated that from 8% to 25% of juvenile coho salmon marked in the upper basin emigrated to the SEE in Freshwater Creek prior to March, and the majority of movement occurred in or about December. There was no tagging program in place upstream of the SEE in Elk River or Jacoby Creek, but we observed the same pattern of new fish arriving in Martin Slough and Rocky Gulch as we observed in Wood Creek, and are confident this illustrates that juvenile coho salmon from Elk River and Jacoby Creek have similar life history patterns to fish from Freshwater Creek.

One of the traits attributed to nomadic coho salmon is their propensity to rear in non-natal streams. Little to no coho salmon spawning takes place in Wood Creek, Martin Slough, or Rocky Gulch, yet we captured juveniles rearing in these areas during the winter and spring. Based on our PIT-tag detections and recoveries, these over wintering coho salmon tend to move around the SEE more than YOY individuals in the summer. For example, we originally tagged juvenile coho salmon in upper Elk River Slough and at specific sites in Martin Slough, and then recaptured them throughout the entire Martin Slough sampling area. We also detected tagged fish moving throughout the Freshwater-Ryan Creek SEE (Table 9). Furthermore, we documented occasional movement between adjacent watersheds by recapturing two 1+ coho salmon in Rocky Gulch one spring that were originally tagged in Jacoby Creek the preceding December. These fish either entered Humboldt Bay to move between watersheds or had been able to traverse over pasturelands during high winter flows. We have even recaptured coho smolts originally tagged in Freshwater Creek in the lower kilometer of Elk River Slough, likely an example of coho salmon moving into tidal slough habitat to forage while rearing in Humboldt Bay on their way to the ocean. Increased connectivity between tributaries and other types of seasonal habitats have been shown to improve winter growth and survival of juvenile coho salmon (Ebersole et al. 2006). It is almost certain that the ability of juveniles to move throughout the SEE of Humboldt Bay has been greatly reduced by levee construction and tide gate installations, both of which have resulted in of loss of watershed connectivity and rearing habitat. In some Oregon estuaries it is thought that loss of habitat and connectivity has resulted in the loss of life history diversity (Bottom et al. 2005).

Juvenile coho salmon captured in the SEE of Freshwater Creek were larger than their upstream cohorts at every life stage. Ricker and Anderson (2011) noted that juveniles were larger at their sampling sites in the SEE than at their traps farther upstream during both fall and spring sampling. Other investigators reported juvenile coho salmon being larger in the SEE compared to those in streams (Tschaplinski 1987, Miller and Sadro 2003, Craig 2010). Also, larger juvenile coho salmon had higher over winter survival than smaller fish (Tschaplinski 1982, Heifetz et al. 1989, Ebersole et al. 2006). The larger size of fish in the SEE is thought to be due to increased food, warmer water temperatures, and lower bioenergetic demands due to low water velocity in these low-gradient ecotones compared to stream habitats. Rebenack et al. (2014) reported that in Freshwater Creek, juvenile coho salmon from the mid-basin were more likely to move to the SEE than were fish from the upper basin. Since fish in the mid-basin were on average larger than those in the upper basin (Figure 7), this movement pattern might have contributed to the larger size of juveniles found in the SEE.

We also noted the average size of YOY coho salmon in the SEE was smaller in years of high YOY coho CPUE (Wallace and Allen 2015), indicating that high density may adversely affect growth in the SEE. This result suggests that restoring historic rearing habitat in the SEE could increase the size of YOY coho salmon rearing in the SEE by lowering density and thereby increasing their overwinter survival. Larger sized salmonid smolts have been shown to have a higher marine survival rate than smaller smolts (Pearcy 1997). Therefore, juvenile coho salmon that have reared in the SEE may survive in the ocean at a higher rate than their stream dwelling cohorts.

The SEE produced a substantial portion of the coho salmon smolts emigrating from Freshwater Creek watershed in 2007 and 2008. Mark-recapture studies carried out by CDFW personnel in the Freshwater Creek SEE during those years indicated the low-gradient 4 km area between the HFAC weir and the Howards Heights trap produced ~40% of the coho salmon spring smolts (Wallace and Allen 2009, Ricker and Anderson 2011). In some other years the majority of smolts originated in the SEE. Additionally, estimates of spring smolt abundance increased at each subsequent downstream counting station. Although Ricker and Anderson (2011) expected this to be the case, the magnitude of increase was not proportional to the linear stream length added by each trap; as a result, smolt estimates increased by up to eight-fold when the SEE was included. Ricker and Anderson (2011) hypothesized that winter was the limiting period for coho smolt production in the stream portion of Freshwater Creek and the SEE was populated after stream carrying capacity is reached. We observed similar life history patterns in the other Humboldt Bay tributaries such as Elk River-Martin Slough and Jacoby Creek-Rocky Gulch. We do not have empirical data demonstrating that the same portions of the SEEs were used by coho salmon smolts. However, based on the relatively large catches of coho salmon in Rocky Gulch—and especially Martin Slough—we suspect substantial portions of smolt production occurs in the SEE of these streams as well.

In Freshwater Creek we detected a positive relationship between adult escapement and subsequent CPUE of YOY coho salmon in the upper slough (Figure 4). The linear relationship with the Y-intercept near zero suggests a density-independent movement rate and we would expect more juvenile coho salmon in the SEE subsequent to years of high adult escapement. The widespread utilization of the SEE by juveniles leads to a number of life history and management considerations. First, the SEE will likely be sparsely populated in the summer by YOY coho salmon following years of low adult escapement, similar to what occurred in the Freshwater Creek SEE in 2008 and 2010 (Table 2). When assessing the success of habitat restoration projects in the SEE after low escapement years, care must be taken to not misinterpret low juvenile coho salmon abundance at the restored sites as indicating project failure when, in reality, it may be due to a lack of seeding. Second, for coho salmon populations that are recovering, it is necessary to take full advantage of high abundance of spawning adults and subsequent offspring and a healthy, restored SEE is needed to provide adequate rearing areas. Third, large numbers of juveniles in the SEE will bias coho salmon smolt estimates low since most trapping sites used to estimate smolt abundance are located upstream of fish rearing in the SEE. Fourth, because juvenile coho salmon abundance in the SEE appears to be dependent on the magnitude of adult spawner escapement, fish abundance may not be the best metric to track trends in estuary recovery. For example, increasing SEE habitat availability or quality with habitat restoration projects could occur during a region-wide downward trend in the sizes of adult runs and result in fewer juvenile fish moving to the SEE independent of conditions occurring there. Assessing the success of these projects and the overall health of the estuary may be better served by using population-independent metrics based on changes in the SEE, such as the amount and types of available salmonid habitat, and the spatial distribution of juvenile coho salmon relative to the availability of habitat.

Due to the extensive use of the SEE by juvenile coho salmon and the perceived benefits resulting from this behavior, numerous habitat restoration projects have been planned, initiated, and completed in the SEE around Humboldt Bay. Results from three completed sites (Wood Creek, Rocky Gulch, and Salmon Creek [the third largest tributary to Humboldt Bay]), indicated that juvenile coho salmon immediately moved into newly accessible streams and man-made off-channel ponds. Fish access to Rocky Gulch had been blocked by tide gates for decades. A new fish-friendly tide gate was installed in December 2004 (Mierau 2005), and by 2007 juvenile coho salmon were found rearing there in winter and spring (Wallace and Allen 2009). Similarly, juveniles moved into newly constructed off-channel ponds in Wood and Salmon creeks during their first opportunity with increased stream flows in late fall (Wallace 2010, Wallace and Allen 2012). The Wood Creek pond has been used by coho salmon from throughout the Freshwater and Ryan Creek basin every winter-spring season since it was built (Wallace 2010, Wallace and Allen 2015). During 2011–12, the first winter-spring season after the Salmon Creek off channel ponds were constructed, CDFW personnel captured more juvenile coho salmon than in the six previous years combined (Wallace and Allen 2015).

These results demonstrate that habitat restoration projects designed to create overwinter habitat and reconnect adjacent stream networks can immediately increase rearing habitat that likely benefits coho salmon populations in portions of the Humboldt Bay SEE, and suggest these measures could provide similar benefits to coho salmon throughout their range in California. By documenting life history strategies of coho salmon and identifying factors that limit their production we can design restoration projects that effectively improve habitat conditions and non-natal rearing potential for juvenile coho salmon.

Acknowledgments

Thank you to E. Ojerholm for being a great field crew leader and to J. Sartori and M. Reneski for their expert fieldwork. Many thanks to M. Zuspan for setting up and maintaining the PIT-tag antenna arrays. Also, thank you to N. Burks, B. Crouch, G. Garman, M. Gilroy, C. Hannon, A. Jeffrey, V. Jimenez, D. Kyle, M. Lomeli, M. McDowall, C. Meredith, G. Morningstar, T. Newhouse, K. Ramey, C. Ramsey, A. Shows, and numerous Americorp volunteers for assisting with fieldwork. Thank you to M. Gilroy for helping with project design, discussing ideas, and sharing knowledge about salmonid ecology. Thank you to A. Moran and H. Lovig for preparing some of the graphics. Thank you to D. Ward, K. Ramey, and an anonymous reviewer for providing many helpful comments that greatly improved the quality of this paper. This project was partially funded by Federal Aid in Sport Fish Restoration Projects F-137-R and F-51-R-67 and the California Department of Fish and Wildlife Fisheries Restoration Grants Program. Fisheries technicians and administrative support were provided by the Pacific States Marine Fisheries Commission under contracts P0810517, P0610522, P0410504, and P0310534. Finally, thank you to the Northcoast Regional Land Trust, Jacoby Creek Land Trust, Humboldt Bay National Wildlife Refuge, the cities of Eureka and Arcata, Green Diamond Resource Company, and numerous private landowners for allowing us to access their properties.

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Received 5 August 2015
Accepted 18 September 2015
Associate Editor was K. Shaffer