Feeding Ecology of Cutthroat Trout in the Salmon River Estuary, Oregon

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Abstract.—Until recently, coastal cutthroat trout *Oncorhynchus clarkii clarkii* were thought to use estuaries primarily as a migration corridor to and from the ocean, rather than as a rearing environment. However, recent research in Oregon's Salmon River estuary has defined an extensive estuarine life history for a portion of the population. This study was designed to assess the diet of coastal cutthroat trout that reared in the Salmon River estuary during the summer 2003. Fifty-five coastal cutthroat trout, ranging in size from 130-400 mm, were collected by beach seine at three locations in the Salmon River estuary from June 18 through August 1. Stomach samples were obtained by gastric lavage and described by taxonomy, total number, and weight. Fish community composition was also recorded at each site. Coastal cutthroat trout fed actively on pelagic and benthic fishes, benthic invertebrates, and some terrestrial insects. Only 4 of 55 cutthroat trout had empty stomachs. Overall, prey availability and diet varied by site. Active selection of various prey items was noted at each location and was site specific. Chinook salmon fry were not selected for, although they were found in stomach samples.

Introduction

Coastal cutthroat trout *Oncorhynchus clarkii clarkii* have among the most complex life history patterns found in Pacific salmonids, and this complexity is exemplified by their migratory behavior (Johnston 1982; Northcote 1997; Johnson et al. 1999). All cutthroat trout are spawned in freshwater, but they exhibit a diversity of rearing patterns ranging from residency to migratory within fresh water (i.e., potamodromy) as well as migration to marine waters (i.e., anadromy). Despite these migratory tendencies, sea-run cutthroat spend most of their life in freshwater and, unlike other anadromous salmonids, migrate to marine waters to feed for only a brief period (rarely more than six months; Trotter 1997). Few, if any, overwinter in marine waters, though they may make repeated excursions during subsequent years. While the marine residence of cutthroat is brief, it remains an important life history phase influencing both growth and survival (Pearcy 1997).

The estuarine environment is of particular importance to sea-run cutthroat trout because they repeatedly migrate to and from marine water. Thus, cutthroat trout spend more time in this environment than other Pacific salmonids. In a comprehensive study of the Nestucca, Alsea, and Siuslaw estuaries, Giger (1972) concluded that although the estuary may be more important for cutthroat trout than for other salmonids, it is used as mainly a "staging ground" for passing to and from the ocean. Other publications (Loch and Miller 1988; Pearcy et al. 1990; Trotter 1997), however, suggest that estuaries likely play a larger role in coastal cutthroat trout development. A population in the Rogue River, Oregon, was found to remain in the estuary, rarely migrating to the ocean (Thomasson 1978). In a recent telemetry study in the Salmon River, Oregon, Krentz (2007) demonstrated that estuarine use by coastal cutthroat trout can be highly variable. Some trout reside in the estuary for the duration of the summer while others stay for only a few days as they pass to and from the ocean. These rearing strategies appeared to be independent of size or age.

Considering that some populations of coastal cutthroat trout use estuaries extensively, it is beneficial to understand their feeding ecology while in estuarine environments. Existing research on this subject is minimal; however, limited but conflicting data have been collected in several locations. Giger (1972a, 1972b) concluded that in the Columbia River estuary cutthroat forage when moving downstream, but their primary food resources are in the ocean. However, Johnston (1982) suggested that the movement of anadromous cutthroat through Minter Creek, Washington, may be timed to prey on migrating juvenile salmonids in the estuary. Giger (1972a, 1972b) also argued that cutthroat trout do not feed in the estuary on the return trip to the spawning grounds. However, other studies (Loch and Miller 1988; Trotter 1997) found that cutthroat trout do feed on the return trip, although perhaps not as extensively

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as on the downstream migration.

Cutthroat trout are thought to be opportunistic feeders (Pauley et al. 1989; Trotter 1997). In freshwater, cutthroat trout diet is dominated by aquatic invertebrates, although terrestrial insects, zooplankton, and fish are consumed when available (Pauley et al. 1989). Out at sea, cutthroat trout prey on a variety of invertebrates including gammarid amphipods, isopods, shrimp, juvenile crab, mysids, and euphausids. They also prey on fish such as sculpins and other small bottomfish, anchovy, stickleback, sand lance, and various species of juvenile salmonids (Loch and Miller 1988; Pauley et al. 1989; Trotter 1997). In the estuary, cutthroat trout diets have been found to include Crangon shrimp, gammarid amphipods, aquatic insects, herring, anchovies, perch, and smelt (Giger 1972b; Loch and Miller 1988; Pearcy et al. 1990). Diet changes from invertebrates to fish as the cutthroat trout move downstream through the estuary (Giger 1972b). In addition, cutthroat trout become more piscivorous as they increase in size (Pauley at al. 1989).

The ocean is thought to provide plentiful food resources for salmonids during the transition from their juvenile to adult stage, hence the advantage of an anadromous lifestyle. However, a significant portion of cutthroat trout in the Salmon River spend little or no time in the ocean and instead remain in the estuary for the entire spring and summer (Krentz 2007). This study was designed to examine the diet composition of coastal cutthroat trout residing in the Salmon River estuary during the summer months. By describing cutthroat diet and feeding ecology in this residence period, we hope to shed some light on why the cutthroat trout exhibit an estuarine life history. We also address how feeding behavior differs by cutthroat trout size and sample location (i.e., habitat and estuary position), and we consider if certain prey are selected.

Methods

Study area.—The Salmon River estuary is located on the north central Oregon coast (45° 01' N, 123° 58' W), approximately 6 km north of Lincoln City (Figure 1). The watershed drains approximately 194 km^2 and forms an 800 ha estuary that extends 6.5 km from the mouth.

We selected three sample locations in the estuary (Figure 1). Site 1, the downstream site, is characterized by eel grass beds and a fringing marsh, adjacent to a deep channel. It is located in the lower estuary, and experienced an average salinity and temperature of 30 ± 9‰ and 14 ± 4ºC, respectively, during the sampling period. Site 2 is a deep channel located at the mouth of an undisturbed marsh (Gray et al. 2002). It is located in the mid-estuary and experienced an average salinity and temperature of 12 ± 7‰ and 18 ± 2ºC, respectively. Site 3 is a deep pool at the mouth of a recently restored marsh (Gray et al. 2002) in the upper estuary. It had an average salinity of 8 ± 6‰ and temperature of 19 ± 3ºC, respectively. Based on telemetry data (Krentz 2007), these three sites represented the primary holding areas for cutthroat trout in the estuary. We collected all data between 18 June and 1 August 2003.

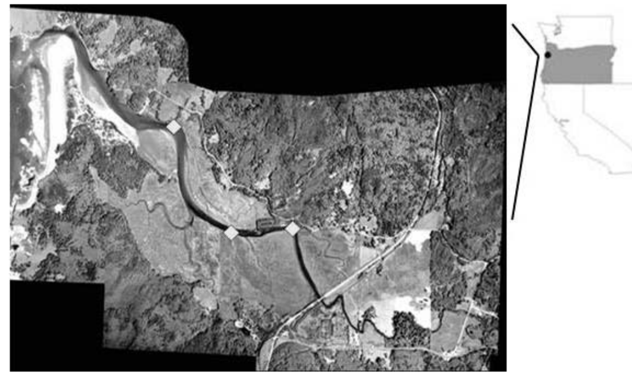

FIGURE1.—Aerial view of Salmon River estuary, located on the north-central Oregon coast approximately 6 km north of Lincoln City. Sample sites are marked by the light colored diamonds. The estuary enters the ocean to the left. Downstream site is site 1, mid-estuary site is site 2, and upstream site is site 3. Highway 101 is the white line that crosses the estuary upstream of the third site. Marsh areas are adjacent to the main channel.

Sampling methods.—The number of cutthroat sampled by site and size class is shown in Table 1. We attempted to sample 15-20 cutthroat trout from each site, and to represent each size class equally (i.e., 130-220 mm, 220-280 mm, and 280-400 mm by fork length; Table 1). Unfortunately, we were unable to sample as many cutthroat trout in the 220-280 size class, only one of which was from the upper site, site 3 (Table 1).

Table 1.—Numbers of cutthroat trout sampled by site and size class.

Site	130-219 mm	220-279 mm	280-400 mm	Subtotal
Lower (Site 1)	7	3	6	16
Mid (Site 2)	10	6	4	20
Upper (Site 3)	9	1	9	19
Subtotal	26	10	19	55

We collected cutthroat trout with a beach seine measuring 38 by 3 m (1.9 cm mesh in the wings) with a bag 3 by 1.5 m (0.6 cm mesh). Cutthroat trout were sedated with MS-222 (50 gm/L) and measured for fork length (tip of snout to caudal fork). Gastric lavage, a common technique in fish diet studies, was used to excavate stomach contents (Foster 1977; Light et al. 1983). A garden pump with soft rubber tubing (4 mm diameter) provided the water pressure to flush stomach contents on to a 500 µm sieve. We did not sacrifice any cutthroat trout because they were part of a larger study by Krentz (2007) and were thus unable to test the efficiency of the technique. However, other studies have demonstrated a very high efficiency (>90%) for trout of similar size (Foster 1977; Meehan and Miller 1978; Light et al. 1983; Gunckel 2001). Stomach contents were stored in ethanol. Other fish species caught in the net were counted and recorded for prey availability data. Additional beach seining was conducted in conjunction with ongoing studies in the Salmon River estuary by Krentz (2007) and Hering (unpublished), and these data were also used to assess prey availability.

Stomach content analysis.—Stomach contents were identified (when possible) and enumerated under dissecting scope. The number of each fish species present was counted, but we recorded only presence and absence data for invertebrate prey due to extensive disarticulation. Total and individual stomach contents were weighed to the nearest 0.1 g to provide relative weights of fish, invertebrate, and terrestrial invertebrate prey groups. Other items, such as rocks, wood, and algae, were also recorded.

Stomach content composition was calculated as percent biomass of differing prey types. A G-stat (Sokal and Rohlf 1981) was used to test for differences in prey species at each site and also among prey species found in stomach samples between sites. Ivlev's electivity index (Strauss 1979) and the log of the odds ratio (Gabriel 1978) were used to test for fish prey species selection (i.e., captured by the 0.6 cm seine mesh) by cutthroat trout. We did not test for selection of invertebrate prey because we had no relative measure of availability of aquatic or terrestrial invertebrates. Ivlev's index is scaled from -1 to +1. The log of the odds ratio is scaled from $-\infty$ to $+\infty$. Infinity is reached either when prey was eaten but not caught in the beach seine (positive), or when prey items were not eaten but were caught in beach seines (negative). For the items that were present in both net and stomachs, the values of the ratio runs from about -10 to +10. The advantage of the log of the odds ratio is that a standard error can be calculated, which allows for tests of statistical significance. Because the results of Ivlev's and the log of the odds ratio were similar, we only present the results from the later. A z-statistic was calculated to test for significance between Ivlev's and log of the odds, according to Gabriel (1978). Data on prey species available at each site, used to calculate electivity, were summarized from seine hauls most similar in time, tide, and location to the capture of each individual cutthroat.

Multivariate analyses were based on ln(x+1) transformed data using the Bray-Curtis distance measure (McCune and Grace 2002). Ordination and significance tests used Canonical Analysis of Principal Coordinates (CAP) (Anderson and Willis 2003). Partial CAP allowed the test of an explanatory (constraining) variable after partialling out (conditioning) the variation related to a covariate. All significance tests used 10,000 permutations of residuals under the full model, stratified by site when necessary (Legendre and Legendre 1998). Analyses were run using the vegan package in R, version 1.8.1 (R Development Core Team 2003).

Results

We sampled stomach contents from 55 total coastal cutthroat trout, 16 cutthroat trout from the lower estuary site, 20 from the mid-estuary site, and 19 from the upper site. Fork lengths ranged from 132-397 mm. The majority of cutthroat trout sampled, 93%, had prey in their stomachs. Of these, 73% had invertebrates, 62% had fish, and 18% had terrestrial insects in their stomachs (Table 2).

Fish and invertebrates co-occurred in 47% of cutthroat trout stomach samples. Of 25 stomach contents with identifiable fish prey, 22 (88%) of those consisted of only one species. The most common fish prey species were northern anchovy *Enaraulis mordax*, staghorn sculpin *Leptocottus armatus*, shiner perch *Cymatogaster aggregata*, and juvenile Chinook salmon *Oncorhynchus tshawytscha* (Figure 2). The most common invertebrate prey taxa were isopods (*Gnorimosphaeroma* spp.) and gammarid amphipods (*Corophium* spp. and *Eogammarus* spp.) (Figure 2). One particular fish (132 mm in length) was captured two days in a row (identified by passive integrated transponder [PIT] tag), and both times had isopods, mysids, and gammarid amphipods in its stomach. Small rocks and plant matter were also common in stomach samples. Cutthroat trout had consumed fish, invertebrate, and terrestrial invertebrate prey at all sites. However, cutthroat trout at the mid-estuary site (site 2) had a higher occurrence of benthic fishes (sculpins and gunnels) and benthic invertebrates (*Corophium* spp. and isopods) in their stomach contents than at either the upper or lower site.

TABLE 2.—Prey items identified in cutthroat stomach samples.

Prey type	Prey taxa
Pelagic Fish	Chinook salmon (*Oncorhynchus tshawytscha*) Northern anchovy (*Engraulis mordax*) Pacific herring (*Clupea harengus*) Shiner perch (*Cymatogaster aggregata*) Surf smelt (*Hypomesus pretiosus*)
Benthic Fish	Pacific staghorn sculpin (*Leptocottus armatus*) Prickly sculpin (*Cottus asper*) Saddleback gunnel (*Pholis ornata*) Flatfish spp. (family *Pleuronectidae*) Pacific sand lance (*Ammodytes hexapterus*)
Estuarine Invertebrates	Isopoda *Eogammarus* spp. *Corophium* spp. *Crangon* spp. Cirripedia Brachyura Zoea Brachyura parts Mysidae Polychaeta Nematoda
Terrestrial Invertebrates	Soldier Beetle (family *Cantharoidae*) Ladybug (genus *Coccinellidae*)

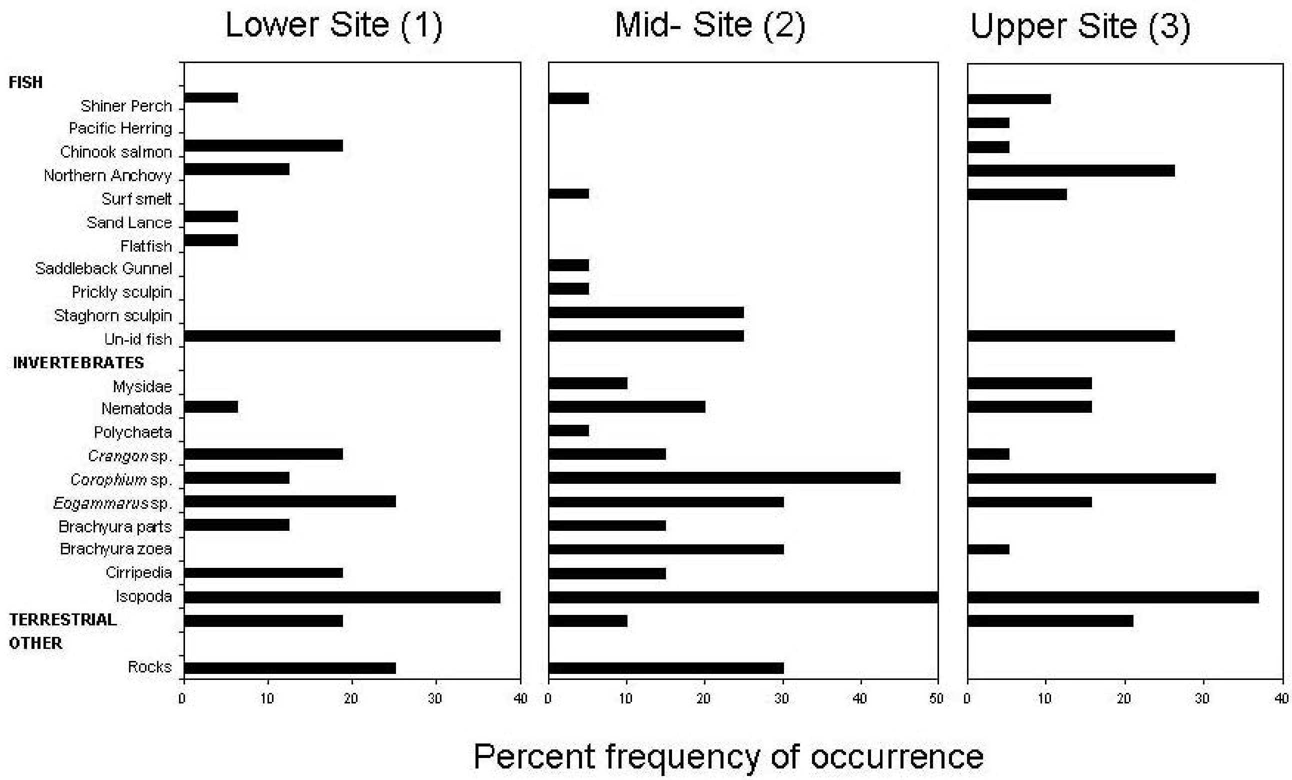

FIGURE 2.—Percentage occurrence of each prey taxa in cutthroat stomach samples by site.

Fish size was positively correlated with the amount of fish and invertebrate prey consumed, but not with the amount of terrestrial species ingested. Percent biomass of fish prey increased significantly with fork length (Spearman's ρ, $r^2 = 0.494$, $p < 0.001$). Percent biomass of invertebrates by fork length varied significantly (Spearman's ρ, $r^2 = -0.381$, $p = 0.004$). There was no significant variation in percent terrestrial biomass by fish size by regression and correlation (Spearman's ρ, $r^2 = -0.128$, $p = 0.353$). When trout were grouped into size classes (130-220 mm, 220-280 mm, 280-400 mm) cutthroat trout in the largest size class ate a significantly higher percentage of fish prey than the smallest size class; they also consumed a significantly lower percentage of invertebrate prey than fish 130-220 and 220-280 mm long (Tukey's HSD pairwise comparison: $p < 0.05$; Figure 3).

No significant relationship existed between sample site and percent biomass of fish, invertebrate, and terrestrial prey consumed (ANOVA: $f = 1.212$, $p = 0.306$; $f = 0.252$, $p = 0.779$; $f = 1.619$, $p = 0.208$, respectively; Figure 4). However, the prey species available and prey species consumed varied significantly between sites ($G_{H(28)} = 133.51$, $p < 0.001$ for prey availability, $G_{H(18)} = 47.82$, $p < 0.001$ for prey consumed; Figure 5).

The multivariate analysis identified similar significant relationships of fish prey in the diets. Cutthroat body length explained a greater amount of variation in diet composition than did salinity or date of stomach sampling when each variable was tested separately (salinity: 8.8%, date of sampling: 13.0%, length: 17.4%; $p < 0.001$). After accounting for cutthroat length, diet composition varied significantly among sites as well (conditioned: 17.4%, constrained: 19.5%; $p = 0.0035$; Figure 6). Axis 1

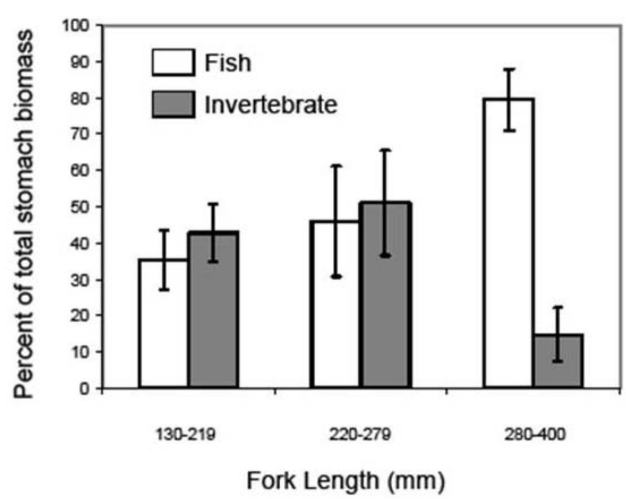

FIGURE 3.—Percent fish and invertebrate prey of total cutthroat trout stomach biomass, by size class of cutthroat trout. Error bars represent standard error.

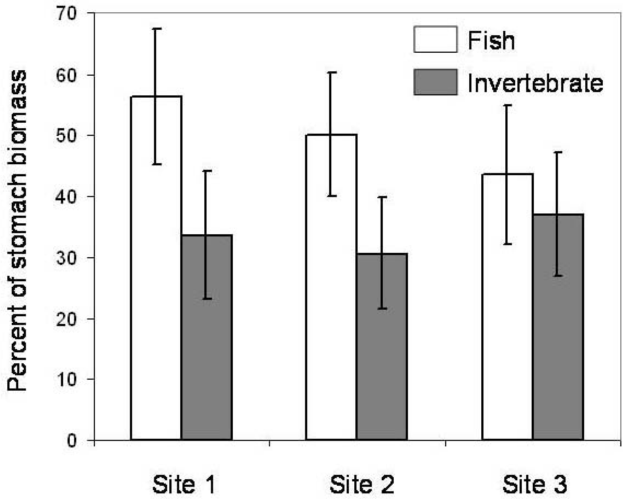

FIGURE 4.—Percent fish and invertebrate prey of total cutthroat stomach biomass, by sample site. Error bars represent standard error.

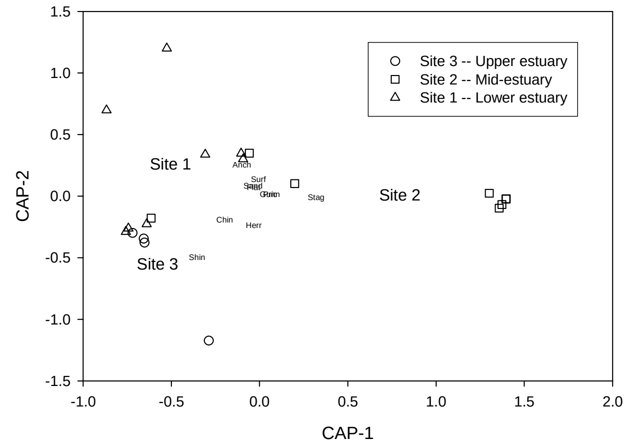

FIGURE 6.—Ordination of diet by site and piscine prey species. Site centroids shown by site labels. Diet of individual cutthroat identified by symbol according to site and prey species (identified by first four letters of common name). Prickly sculpin and saddleback gunnel overlap near the center, as do flatfish and Pacific sandlance.

explained the variation between fish diets at site 2 and sites 1 and 3. Axis 2 separated the variation in diet between sites 1 and 3. Northern anchovy and surf smelt were associated with diets at site 1, Pacific staghorn sculpin with site 2, and shiner perch, Chinook salmon, and Pacific herring with site 3.

Cutthroat trout demonstrated preference for certain fish prey (z-test on log of the odds ratio: $p < 0.001$; Table 3). The log of the odds ratio indicated that at the lower site (site 1) cutthroat trout preferentially selected anchovy, shiner perch, and surf smelt. Staghorn sculpin and surf smelt were selected at the mid-estuary site (site 2), and anchovy, Pacific herring, and juvenile shiner perch at the upper site (site 3). Juvenile Chinook salmon were abundant in beach seine catches at every site, but were not eaten proportionally to their abundance in the estuary at the mid- and upper sites. Numerous fish prey were collected by beach seine in the estuary, but not consumed by cutthroat trout. Table 3 displays the complete electivity results for fish prey, and prey availability is shown in Figure 5.

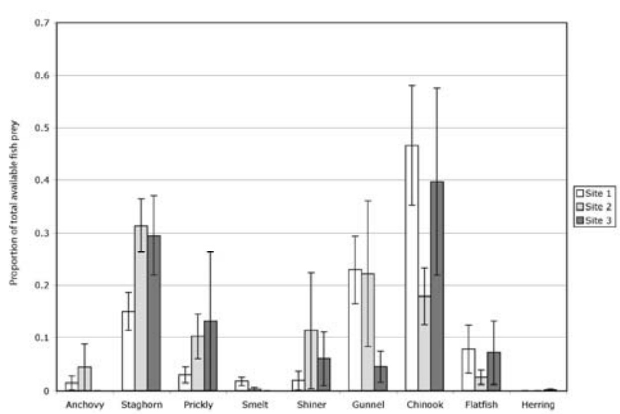

Figure 5.—Composition of available fish prey species at each site, based on seine net capture (n = 24). Error bars represent standard error.

Discussion

Smaller cutthroat trout in the estuary fed on a higher percentage biomass of invertebrate than fish prey, while the converse was true of larger cutthroat (Figure 3). This

TABLE 3.—Fish species selected for and against by cutthroat trout according to the log of the odds ratio at each site. Species were only included if present in significant numbers and consumed by cutthroat trout at one of the three sites. Negative values represent selection against and positive represents positive selection for an item. Negative infinity indicates that prey were available but not eaten, positive infinity indicates that prey were eaten but not collected by beach seine. Significant values ($p < 0.05$) are highlighted in gray. Blank cells indicate that a species was not collected by beach seine or stomach sample at a site.

Species	Lower estuary	Mid-estuary	Upper estuary
Juvenile shiner perch	+1.8	- 0.6	+3.4
Pacific herring	- ∞		+2.1
Chinook salmon	- 0.5	- ∞	-2.4
Northern anchovy	+2.9		+ ∞
Surf smelt	+2.5	+3.9	
Flatfish	- 0.2	- ∞	- ∞
Saddleback gunnel	- ∞	- 0.3	- ∞
Prickly sculpin	- ∞	+ 0.5	- ∞
Pacific staghorn sculpin	- ∞	+1.1	- ∞

increase in piscivory with size appears to be a pattern common among cutthroat (Pauley et al. 1989). Invertebrates, however, remained an important part of the diet of large fish (280-400 mm) in the estuary, comprising about 15% of their diet in terms of weight. Eleven out of the 18 fish in the largest size class which had items in their stomachs contained invertebrates. Of these eleven, two of the samples were comprised solely of invertebrate prey items.

In late July, a large school of northern anchovies moved into the upper site. Six cutthroat trout were sampled from that site during this time, all between 297 and 400 mm, and all except one had anchovies in their stomachs. Such opportunistic feeding is thought to be characteristic of cutthroat trout (Giger 1972b; Loch and Miller 1988; Pauley et al. 1989). On this occasion, the water salinity at the upper site was 37‰ due to a strong tide and the temperature was 11ºC, conditions which mimic that of the offshore ocean. Although marine species are common at the upper site during late summer, the presence of northern anchovy was not observed in such abundance in previous years (T. Cornwell, Oregon Department of Fish and Wildlife, personal communication).

Giger (1972b) noted that the diet of cutthroat trout shifted from one dominated by insects to one dominated by sand shrimp and fish as the cutthroat moved downstream through the estuary. This change was attributed to differences in prey availability in different estuary regions (see also Trotter 1997). The present study indicated that prey species consumed varied significantly among sites. However, fish, invertebrates, and terrestrial invertebrates were consumed at all locations (Figures 2 and 4).

Site-specific feeding behavior by cutthroat trout in relation to habitat conditions was evident. Pelagic fish were the main fish prey at sites 1 and 3, while benthic fish were the primary fish prey at site 2. All aquatic invertebrates found in stomach samples in this study were benthic infauna, except mysids, which are considered epibenthic. The predominance of benthic invertebrates and fish prey in the diet of cutthroat trout at site 2, as well as a higher frequency of rocks within stomachs, suggests that these cutthroat trout were feeding primarily on the bottom unlike cutthroat trout at the other two sites. The large marsh channel system which enters at site 2 is known to support a higher average density of benthic macroinvertebrates than other marsh areas in the estuary (Gray et al. 2002). No variation in the consumption of terrestrial prey was observed in relation to cutthroat body size or sample site. However, 20% of cutthroat had been feeding on terrestrial invertebrates, which are an energy rich and readily available food source, particularly at site 3 (Gray et al. 2002).

Ivlev's electivity index (Straus 1979) and log of the odds ratio (Gabriel 1978) were used to assess if cutthroat trout were selecting for certain fish prey at each site. It is important to recognize that our sample sizes are small, and also that sampling bias may exist because prey availability was determined by seine netting. Capture efficiency with a 0.6 cm mesh beach seine is lower for benthic than for pelagic species, although fish as small as 35 mm are effectively sampled at this mesh size (Lyons 1986). We were not able to measure invertebrate availability at each site, which is unfortunate because in many cases invertebrate prey dominated stomach contents. Despite this, we feel that these electivity data provide insight regarding fish prey selectivity, and match what we expected based on observations from the field. By our electivity results (Table 3), cutthroat trout selected different prey fish in different locations in the estuary even though availability was similar. Ivlev's electivity index and the log of the odds ratio showed that juvenile shiner perch, northern anchovy, Pacific herring, and surf smelt were selected for at sites 1 and 3, and that staghorn sculpin and surf smelt were selected for at site 2. Cutthroat trout did not feed on the available Chinook salmon fry or shiner perch at site 2. Cutthroat trout at site 2 were oriented toward benthic food sources, but at sites 1 and 3 pelagic fish were preferred. Chinook fry, juvenile flatfish, saddleback gunnel, and sand lance were not selected for. Thus, while cutthroat may appear opportunistic in their feeding behavior at times (e.g., foraging on a pulse of available northern anchovies), habitat can influence their prey selectivity.

Four cutthroat trout had been feeding on Chinook salmon fry. Of these four, the smallest cutthroat trout was 268 mm, and the other three were 338, 351, and 374 mm. One additional occurrence was noted the following year when a cutthroat trout was collected containing a PIT tag that had been placed in a Chinook fry (D. Hering, Oregon State University, personal communication). It is debatable how important juvenile salmonids are to cutthroat trout diet. Trotter (1997) concluded that predation on salmonids by cutthroat trout "seems to be situational." He cites four articles where little or no predation on salmonids was recorded, but two others that list young salmonids as a principal food source. Our electivity results showed that although occasional predation on salmonids was occurring, they are not a preferred food source for cutthroat trout despite the abundance of Chinook fry in the estuary (frequently the most common fish species caught in our nets). Only large cutthroat trout were observed to have fed on Chinook fry, even though cutthroat of all sizes were capable of consuming fish larger than the fry.

The Salmon River estuary provides high quality habitat during an important phase in the life cycle of anadromous cutthroat trout. The estuary supports invertebrate, terrestrial, and fish prey that are important components of cutthroat diet. It may also provide relief from many ocean predators, such as Pacific hake, spiny dogfish, sub-adult salmon, and seals (Giger 1972b). Given the ample prey resources and potentially reduced risk of predation in the estuarine environment, a life history that utilizes these habitats may be quite advantageous for coastal cutthroat trout. Johnston (1982) hypothesized that certain populations of coastal cutthroat trout may reside in streams longer due to the availability of eggs from spawning salmon. In this way, the cutthroat are able to take advantage of a plentiful food source while also avoiding exposure to marine predators. We hypothesize that similar pressures may encourage longer estuarine residences for the Salmon River cutthroat trout.

Our findings differ from previous studies that have concluded that the estuary has little influence in cutthroat trout subsistence. Giger (1972b) "discarded" an estuarine diet study of cutthroat trout in the Nestucca, Alsea, and Siuslaw estuaries because it appeared that little or no feeding took place in the summer and fall. However, the Salmon River estuary may be unique among contemporary Pacific Northwest estuaries because of its abundant marsh habitat (Figure 1), much of which has been restored in the past 30 years. These marshes provide productive habitat for many of the prey species upon which coastal cutthroat trout feed (Gray et al. 2002; Bottom et al. 2005). Most Pacific Northwest estuaries have experienced habitat loss due to human activities such as development and channel dredging. Perhaps it is the complex and productive habitat of the Salmon River estuary that encourages and sustains an estuarine life strategy for coastal cutthroat trout.

Conclusions

Cutthroat trout in the Salmon River estuary feed actively during the summer months. The estuary supports a variety of prey species, both invertebrate and fish, which are consumed by cutthroat trout of all sizes. Invertebrates constituted a larger portion of the diet of small cutthroat trout while the larger trout were more pisciverous. As most previous studies have suggested, cutthroat trout feed on most types of available fish and invertebrates; however, our study found that they do show preference towards certain species at each site. No significant differences were noted in the amount of fish, invertebrate, and terrestrial invertebrate prey consumed by site, although variation in prey species consumed was noted and is attributed to differences site-specific habitat.

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