Abstract.– Coastal cutthroat trout and steelhead, which are sympatric over much of their range along the Pacific coast of North America, have different behaviors in both freshwater and the ocean. Juveniles of both species were caught in purse seines off the Oregon and Washington coasts during the early summer, sometimes over 46 km offshore. However, both species were absent from catches in September. Cutthroat apparently returned to freshwater, whereas steelhead migrated far offshore during late summer. Ocean growth rates of smolts of both trouts were similar, about 1 mm per day; but since cutthroat spend little time in the ocean, they are small at maturity. This is possibly an adaptation related to spawning short distances from the ocean or in small tributaries upstream of the spawning and rearing habitats of other anadromous salmonids. Cutthroat trout fed primarily on fishes, but steelhead had a more varied diet in coastal waters, consuming fishes but also euphausiids and other crustaceans.

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Distribution and Biology of Juvenile Cutthroat Trout *Oncorhynchus clarki clarki* and Steelhead *O. mykiss* in Coastal Waters off Oregon and Washington

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Two species of anadromous trout are native to the Pacific coast drainages of North America: *Oncorhynchus c. clarki* (formerly *Salmo c. clarki*), the coastal cutthroat trout, and *O. mykiss* (formerly *Salmo gairdneri* and *S. mykiss*), the steelhead and Kamchatkan trout (Smith and Stearley 1989). The coastal cutthroat trout ranges from northern California to southeastern Alaska. The native range of the steelhead trout was from the Alaska Peninsula to Baja but now is found only as far south as central California (Carl et al. 1959, MacCrimmon 1971, Scott and Crossman 1973).

Because these two trout species are sympatric over much of their range (Scott and Crossman 1973, Behnke 1979) behavioral and ecological differences are of special interest. Coastal cutthroat select small tributaries for spawning, rarely over 160 km inland, whereas steelhead prefer larger streams and sometimes migrate long distances from the ocean. Coastal cutthroat usually spawn slightly earlier in the year (January–March) than steelhead (February–April) (Needham and Gard 1959, Withler 1966, Hartman and Gill 1968, Scott and Crossman 1973, Johnston 1982). These differences in location and time of spawning apparently help maintain reproductive isolation between these species (Needham and Gard 1959, Trotter 1989).

Anadromous wild stocks of both species of trout usually spend 2–4 years in freshwater before smoltification and downstream migration to the ocean, while hatchery stocks commonly migrate to the sea after one year in freshwater. Downstream migrations of smolts of both species usually peak in April or May (Chapman 1958, Lowry 1965, Withler 1966, Armstrong 1971, Giger 1972, Sutherland 1973, Okazaki 1984, Dawley et al. 1985, Loch and Miller 1988) or in late May or early June in Alaska (Armstrong 1971).

Our knowledge of the marine life history and ecology of steelhead and cutthroat trout is meager. In this paper we describe the distribution and movements, age and size distribution, sex ratios, and food habits of juveniles of these species in coastal waters off Oregon and Washington as determined by purse seine catches, discuss the differences between these species, and speculate on their adaptive significance.

Methods

Cutthroat trout and steelhead were captured in purse seines in the northeastern Pacific Ocean during May–September, 1980–85. Data from 1981–85, the years of most extensive sampling, are the basis for most of this paper (see Pearcy and Fisher 1988, for sampling details). A total of 992 quantitative seine sets were made with a 457–495 m seine with 32-mm (stretch measure) mesh that fished to depths of 20–65 m. Sets were made along east-west transects off Oregon and Washington (43°00'N to 48°21'N) at 9.3 km (5 n.mi.) intervals out to about 50 km offshore (Fig. 1). During July 1984, we sampled over a broader area, from northern California (40°32'N) to Vancouver Island (50°26'N).

Trout were identified, measured (fork length, FL), examined for marks, and either released or preserved by freezing at sea. A total of 15 cutthroat and 8 steelhead were tagged with Floy tags and released. In the laboratory ashore, the preserved fish were measured, weighed, scales were removed, stomachs excised, and gonads were examined.

Scales from cutthroat trout and steelhead were collected from an area 1–3 scale rows above the lateral line along the diagonal scale row from the insertion of the dorsal fin (Clutter and Whitesel 1956). Scales were mounted on gummed cards from which acetate impressions were made. The impressions were magnified 88×. All measurements were made in the anterior half of the scale along an axis 20° ventrad to the long axis. Ages of smolts at ocean entrance were estimated by counting the bands of narrowly spaced or broken circuli (interpreted as winter annuli) in the freshwater growth zone of the scale. These freshwater ages are estimates because occasionally "checks," which were difficult to interpret, occurred in the freshwater growth zone and few scales from fish of known freshwater age were available for comparison. The abrupt change from relatively narrowly to widely spaced circuli indicated the transition from freshwater to ocean growth. Subsequent zones of narrowly spaced circuli or resorption on cutthroat trout scales were interpreted as evidence of slow growth from reduced feeding or spawning in freshwater [see Sumner (1962, 1972) and Loch and Miller (1988) for scale interpretations and photographs]. All juvenile steelhead collected were in their first summer in the ocean and had not yet spawned.

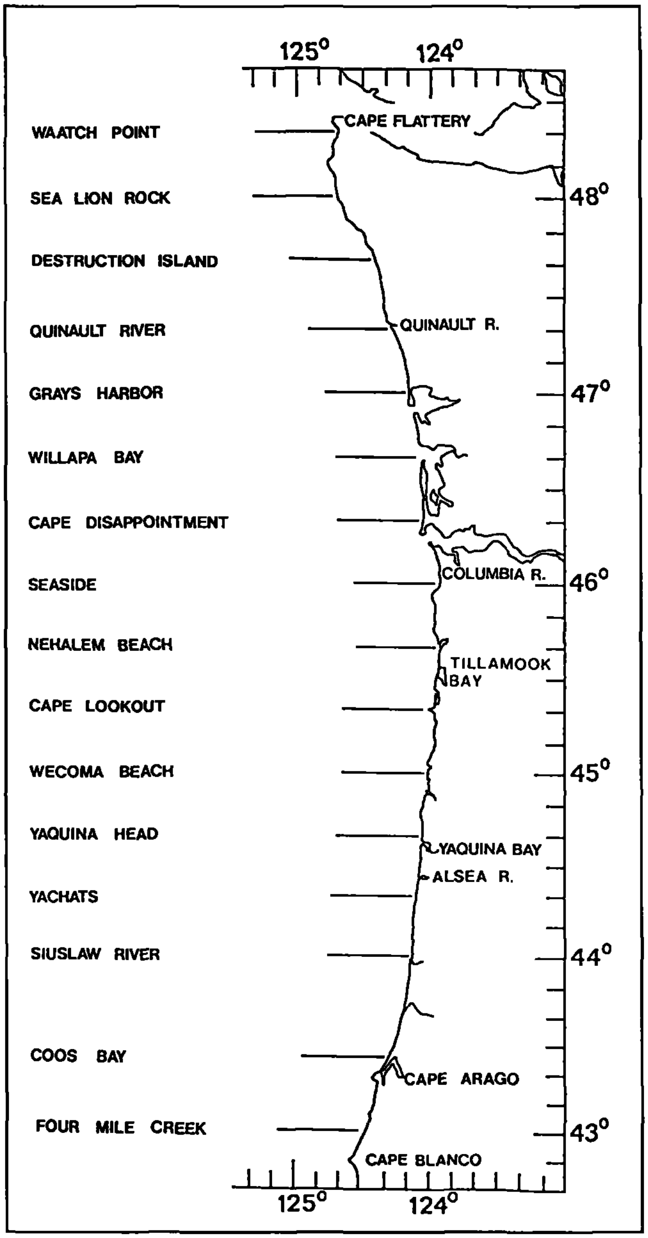

Figure 1
Location of purse seine transect lines off Oregon and Washington.

Size at ocean entrance of cutthroat and steelhead trout caught during their first ocean summer was back-calculated using the method of Lee as described in Carlander (1981):

$$Li = a + ((Lc - a)/Sc) \cdot Si,$$

where Li = FL (mm) at time of ocean entry
Lc = FL (mm) when captured
Sc = total scale radius (mm at 88×)
Si = scale radius at time of ocean entry

a = the y intercept of the regression of FL on scale radius.

The y intercepts (a) for each species were determined from the geometric mean regressions of FL and scale radius (Ricker 1973) from juvenile fish caught in the ocean (cutthroat repeat spawners excluded):

Steelhead
FL(mm) = 51.1 + 1.69 · Sc (mm at 88×), n = 84, r = 0.73, FL range = 143–288 mm

Cutthroat
FL(mm) = 62.1 + 2.26 · Sc (mm at 88×), n = 101, r = 0.70, FL range = 175–369 mm.

Sc-FL relationships for both species appeared linear over the length ranges of fish examined. Back-calculation of size at ocean entrance using natural logarithm transformations of FL and Sc (Bartlett et al. 1984, Hooten et al. 1987) produced only very small differences ($\bar{x}$ 1 mm) in back-calculated lengths compared with untransformed data.

We estimated ocean growth for each steelhead and cutthroat trout by subtracting the back-calculated FL at time of ocean entry from the FL at time of capture in the ocean. Growth rates in the ocean of individual fish were estimated from ocean growth back-calculated from scales divided by estimated days in the ocean. To arrive at estimates of time spent in the ocean we used dates of ocean entry corresponding to the beginning, middle, and end of the period of smolt migration into the ocean, yielding several estimates of growth rate for each fish. Seaward migration of cutthroat trout smolts through the Columbia River and coastal Oregon estuaries generally takes place from late March or early April through May (Giger 1972, Loch and Miller 1988, Dawley et al. 1985), with maximum numbers of smolts occurring in the Alsea estuary in the second week of May (Giger 1972). By the end of May very few cutthroat trout smolts were found in the Alsea estuary (Giger 1972). Almost all steelhead smolts passed river kilometer 75 in the Columbia River estuary between 15 April and 15 June, with half the migration completed by the third week in May (Dawley et al. 1985). We used ocean entry dates of 1 April, 1 May, 10 May, and 31 May to estimate growth rates of cutthroat trout, and 15 April, 1 May, and 17 May to estimate growth rates of steelhead. Although ocean entry of steelhead smolts probably continued until about the middle of June, almost all of our catch of steelhead occurred before 15 June.

We also estimated average growth rate of cutthroat trout from the slope of the regression of back-calculated ocean growth on julian date, a method in which no assumptions are made about a precise time of ocean entry. This method was possible because captures of cutthroat in the ocean extended well past the period of smolt entry into the ocean.

Stomach contents were preserved in 10% buffered formalin, transferred to 70% ethanol prior to examination, and weighed to the nearest mg after removal of excess moisture. Contents were examined with a dissecting microscope and were identified to the lowest possible taxon. Total lengths of intact fish prey were measured to the nearest mm. Percent frequency of occurrence in non-empty stomachs (F), percent of the total number of prey organisms (N), and percent of the total wet weight of prey organisms (W) were determined and combined in the Index of Relative Importance (IRI = F(N + W)). Dietary overlaps were calculated from a Percent Similarity Index (= Σ minimum percent weights of taxa in common between two groups of fish). A total of 67 cutthroat (<300 mm in length) and 98 steelhead stomachs were examined from the collections made in 1980–85. The food habits of 48 larger (>300 mm) cutthroat collected during this study were presented by Brodeur et al. (1987a).

Results

Abundance

A total of 163 cutthroat and 134 juvenile steelhead trout were collected during our cruises in 1981–85. These species combined comprised about 3% of our catches of juvenile salmonids (Pearcy and Fisher In press). Cutthroat and steelhead trout were captured from May through August, and occurred in 0–30% and 2–24%, respectively, of the seine sets during these months (Table 1).

Frequencies of occurrence and catches per set of steelhead were generally highest in May and June and were much lower in July and August (Table 1). Steelhead were absent in September of all years. Abundances of cutthroat trout in 1981, the year of most regular sampling, were highest in July and about the same in May, June, and August. Like steelhead, cutthroat trout were absent in September of all years (Table 1).

Distributional trends

In most years, average catches of cutthroat trout were higher in the region off southern Washington and northern Oregon, near the mouth of the Columbia River (Zone B), than off northern Washington (Zone A) or Oregon south of the Columbia River (Zone C) (Table 2). No obvious latitudinal trends were noted

Table 1

Percent frequency of occurrence (FO), mean catch per set (CPS), and number (*n*) of juvenile cutthroat and steelhead trout caught in purse seine collections, 1981-85, off Oregon and Washington. (S indicates total number of purse seine sets by month.) No steelhead or cutthroat trout were collected in September 1982, 1983, or 1984 (*n* = 38, 51, and 63 sets, respectively). NS indicates no sets were taken during those months.

	May S = 208			June S = 327			July S = 130			August S = 66		
	FO	CPS	*n*	FO	CPS	*n*	FO	CPS	*n*	FO	CPS	*n*
Cutthroat												
1981	13	0.29	18	9	0.19	13	30	0.61	41	12	0.21	14
1982	5	0.13	8	14	0.16	9	NS	NS	NS	NS	NS	NS
1983	9	0.13	7	7	0.14	8	NS	NS	NS	NS	NS	NS
1984	NS	NS	NS	6	0.11	7	3	0.05	3	NS	NS	NS
1985	25	0.46	13*	19	0.28	22	NS	NS	NS	NS	NS	NS
Steelhead												
1981	22	0.51	32	15	0.37	25	7	0.07	5	2	0.02	1
1982	24	0.52	32	4	0.04	2	NS	NS	NS	NS	NS	NS
1983	7	0.07	4	3	0.03	2	NS	NS	NS	NS	NS	NS
1984	NS	NS	NS	8	0.12	8	6	0.08	5	NS	NS	NS
1985	18	0.29	8*	6	0.13	10	NS	NS	NS	NS	NS	NS

*Late May and early June sampling off the Columbia R. mouth.

Table 2

Average catch per set of cutthroat/steelhead trout in purse seine sets off Oregon and Washington, during May, June, and July combined, 1981-85 (number of sets in parentheses). NS = no samples.

Zone	1981	1982	1983	1984	1985
A Cape Flattery to Grays Harbor, WA	NS NS	0.04/0.46 (26)	0.05/0.08 (37)	0/0.15 (33)	0/0.10 (20)
B Willapa Bay, WA to Nehalem, OR	0.58/0.54 (111)	0.16/0.31 (45)	0.21/0.03 (33)	0.32/0.16 (25)	0.50/0.15 (54)
C Tillamook Bay to Cape Blanco, OR	0.09/0.02 (86)	0.19/0.17 (47)	0.14/0.47 (43)	0.02/0 (48)	0.23/0.23 (34)
D Extended cruise					
Swiftsure Bank to Winter Harbor, B.C.				0/0 (15)	
Cape Blanco, OR to False Cape, CA				0/0.5 (8)	

for steelhead. Steelhead were captured as far south as northern California during the extended cruise of July 1984.

The highest average catches of both cutthroat and steelhead trout occurred 37.2-46.3 km offshore (Table 3). Low catches of both species were found in the zone closest to shore (<9.3 km). Catches of cutthroat were high 37.2-46.3 km offshore only in May and June 1985, when juvenile coho salmon were also found far offshore (Fisher and Pearcy 1985). In other years highest catches of cutthroat were 9.4–27.8 km offshore, inshore of maximal steelhead catches. The zone of highest average catches for all years was characterized by a mean sea surface temperature of 13.4°C (standard deviation, SD, 1.4), mean surface salinity of 28.6‰ (SD 4.3) and secchi depth of 5.4 m (SD 2.2). The low surface salinities in areas where steelhead and cutthroat trout were abundant indicate the influence of freshwater, often the Columbia River plume. Detailed spatial information on catches is given by Pearcy and Fisher (In press) by cruise.

Table 3

Mean catch per set of cutthroat and steelhead trout and standard deviation at varying distances from the Oregon/Washington coast, 1981–85, giving equal weight to each cruise (15 cruises sampled inshore of 46 km, except 9 cruises at 46.4–55.6 km, and 2 cruises at >55.6 km).

Distance offshore:	km n.mi.	<9.3 <5	9.4–18.5 5–10	18.6–27.8 10–15	27.9–37.1 15–20	37.2–46.3 20–25	46.4–55.6 25–30	 >55.6
Cutthroat	$\bar{x}$	0.09	0.25	0.17	0.15	0.33	0.03	0.10
	SD	0.09	0.26	0.25	0.28	0.61	0.10	0.14
Steelhead	$\bar{x}$	0.03	0.09	0.16	0.23	0.52	0.19	0
	SD	0.06	0.09	0.23	0.36	0.81	0.38	—

Table 4

Release and recapture data for tagged cutthroat and steelhead trout off Oregon and Washington.

Release			Capture		Days between release and recovery	Distance N/S of release (km)	Tagged	Recovered
Date	Location	Code	Date	Location			- - - - FL (mm)- - - -	
Cutthroat								
12 June 85	Yaquina Head	Floy	25 July 85	Siuslaw R.	43	72 S	294	—
18 June 85	Cape Disappoint.	Floy	Fall 85	Umpqua R.	—	290 S	295	—
Steelhead								
27 March–22 May 81	Quinault R., WA	050758	9 June 81	Leadbetter Pt., WA	18–74	85 S		172
4 May 81	Clearwater R., ID	102252	21 May 81	Warrenton, OR	17	9 S		206
14 May 82	Quinault R., WA	051043	31 May 82	Cape Lookout, OR	17	269 S		185
4 May 84	Clearwater R., ID	051335	10 June 84	Cape Disappoint.	37	9 N		194
22 June 83	Cape Disappoint.	Floy	9 Sept. 83	Jones Beach, Col. R.	79	11 S	445	495

Tag recoveries

Two of the cutthroat trout tagged with Floy tags on our cruises in 1985 were recovered by fishermen, one 43 days after release 72 km south of the tagging location and the other 290 km south of the tagging location (Table 4). We also caught four hatchery coded-wire tagged steelhead smolts in the ocean 17–74 days after hatchery release. The two released in the Clearwater River, Idaho, were captured close to the mouth of the Columbia River where they entered the ocean. Two fish released in the Quinault River, Washington, were recovered 85 km and 269 km south of where they entered the ocean. Movements to the south by these two steelhead and the cutthroat trout may have been related to advection of surface waters during the upwelling season (Pearcy and Fisher 1988).

Of the eight maturing steelhead tagged, one (445 mm FL) tagged off Cape Disappointment near the mouth of the Columbia River was recaptured 79 days following its release at 495 mm FL in the Columbia River. Its growth rate between release and recapture was 0.63 mm/day.

Age, lengths, and sex ratios

Of the 110 cutthroat trout with readable scales, 32%, 45%, 19%, and 3% migrated to sea for the first time after one, two, three, and four winters in freshwater (ages 1., 2., 3., and 4.)*, respectively (Table 5). This is a younger age distribution than found by Giger (1972) for wild cutthroat trout from coastal Oregon river systems, but similar to that found by Loch and Miller (1988) in the ocean off the Columbia River mouth. Most of the age 1. cutthroat we caught probably originated from hatcheries (Loch and Miller 1988), including hatcheries on the Columbia River.

Most cutthroat were immature or maturing fish on their first ocean migration (age .0). Only eight fish had scales that showed evidence of reduced growth (a

* Age designation follows that recommended by Koo (1962), and used by others (Godfrey et al. 1975, Hartt and Dell 1986), where the numbers before and after the decimal point refer to winters spent in freshwater prior to first migration to the ocean and winters spent in the ocean, respectively. Ages 1., 2., 3., etc. designate the freshwater age of a fish without reference to its ocean age.

Table 5

Freshwater age* and number of repeat spawners, as determined from scale analysis, and lengths of cutthroat and steelhead trout caught in ocean purse seines off Oregon and Washington.

	Cutthroat					Steelhead			
			Fork length (mm)					Fork length (mm)	
Month	Freshwater age	No. of fish	$\bar{x}$	SD	No. repeat spawners	Freshwater age	No. of fish	$\bar{x}$	SD
May	1.	10	267	46.1	2	1.	35	216	32.5
	2.	12	258	38.7	1	2.	19	185	17.2
	3.	7	279	27.9	1	3.	7	204	17.9
	4.	1	284	—	0	4.	0	—	—
June	1.	13	280	57.4	2	1.	17	209	28.7
	2.	16	282	48.0	1	2.	7	225	36.2
	3.	8	314	16.1	0	3.	2	257	31.8
	4.	2	271	8.5	0	4.	0		
July	1.	10	284	40.9	0	1.	1	260	—
	2.	16	299	34.8	0	2.	1	246	—
	3.	5	336	27.2	1	3.	0		
	4.	0	—	—	0	4.	0		
August	1.	3	321	10.1	0	1.	0		
	2.	6	316	17.9	0	2.	0		
	3.	1	314	—	0	3.	0		
	4.	0	—	—	0	4.	0		
Total		110			8		89		

* See text footnote, p. 701, for explanation of age designation.

winter annulus or spawning check) after initial ocean entrance ("repeat spawners," Table 5). Six of these had apparently made one previous migration from the ocean to freshwater, and two had made two previous trips to freshwater. All of these fish measured 335–380 mm FL except for one 279 mm FL fish. Half of the repeat spawners had first entered the ocean after one winter in freshwater (age 1.). Seven of the eight prior spawners were collected in May or June, probably soon after reentering the ocean.

All juvenile steelhead caught in the ocean were in their first ocean summer (age .0). Of the 89 steelhead that had readable scales, 60%, 30%, and 10% were ages 1.0, 2.0 and 3.0, respectively (Table 5). Ten of 11 steelhead caught with clipped adipose fins, probably denoting hatchery origin, were age 1.0. Since most wild steelhead enter the ocean after two or three winters in freshwater and most hatchery steelhead after only one winter (Chapman 1958, Withler 1966, Pauley et al. 1986), the majority of fish we caught were probably of hatchery origin.

Length ranges were broad for both cutthroat trout and steelhead during each month (1981–85 combined, Fig. 2). This may have resulted from variable size and age of smolts entering the ocean (Loch 1982, Dawley et al. 1982, Bottom et al. 1984, Ward and Slaney 1988) or variable growth rates. During downstream migration, the length ranges of individual hatchery groups of steelhead smolts can be very broad. For example, Dawley et al. (1986) found length ranges of 150–270 mm FL and 110–240 mm FL for two groups sampled in the upper Columbia River estuary.

Back-calculated length at time of ocean entry of cutthroat trout averaged 241 mm FL, but was quite variable (SD 38 mm, $n = 101$, repeat spawners excluded). Age 3.0 fish tended to be larger at time of first ocean entry than younger fish or age 4.0 fish (average back-calculated FL at ocean entry = 231, 239, 264, and 244 mm FL for age 1.0, 2.0, 3.0, and 4.0 fish, respectively). Our average back-calculated lengths at ocean entry for cutthroat trout caught at sea were larger than those back-calculated by Giger (1972) for wild cutthroat of the same age from the Alsea, Nestucca, and Siuslaw Rivers (239 vs. 210 and 264 vs. 239 mm FL for age 2.0 and 3.0 fish, respectively). However, the mean length at ocean entry estimated by Giger for all freshwater age groups and for all three river systems combined (233 mm FL) by Giger was fairly close to our average (241 mm FL).

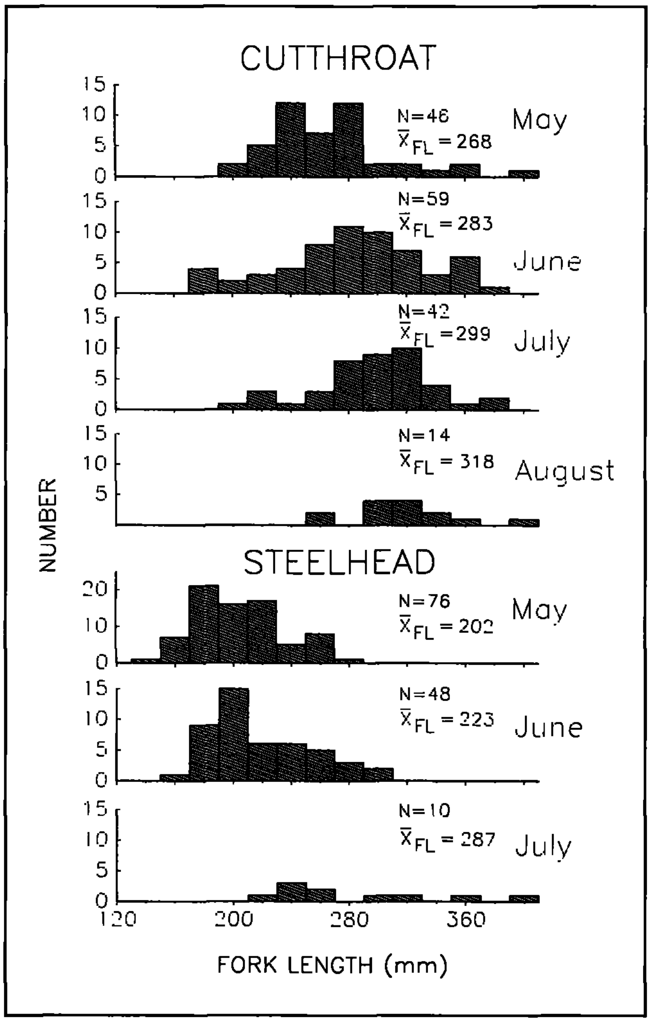

Figure 2
Size-frequency distributions of cutthroat and steelhead trout, by month, 1981-85 combined.

Mean back-calculated FL at time of ocean entry for steelhead was 199 mm (197 mm and 200 mm for fish caught in May and June, respectively) and was quite variable (SD 29 mm, n = 84). These estimated lengths at time of ocean entry were similar to the mean lengths of steelhead smolts caught during downstream migration in the Columbia River (~200 mm, Dawley et al. 1985, their figs. 4–10), and similar to those estimated by Narver (1969, 1974) for steelhead smolts in two British Columbia river systems (182 and 190 mm FL), but were larger than mean lengths of all ages of wild smolts from two Washington streams (156 and 165 m FL; Loch et al. 1988).

The mean lengths of both species increased during the summer. This suggests either growth in length during this time period or higher availability of larger fish later in the summer (Loch 1982, Dawley et al. 1982).

Mean lengths of cutthroat trout caught in the ocean in July and August (299 and 318 mm FL, respectively) were similar to mean lengths of age 2. and 3. cutthroat trout (305 and 323 mm FL, respectively) caught in coastal Oregon estuaries from July through September on their initial spawning migrations (Giger 1972).

More male than female cutthroat were captured, but fewer male then female steelhead were caught. However, the respective sex ratios of 1.3:1 and 0.7:1 were not statistically different from 1:1 (p>0.1, chi-square test). None of the cutthroat trout examined had enlarged testes or ovaries (>1% of body weight), which is expected since cutthroat spawn in the winter-spring period.

Ocean growth

Of cutthroat trout caught in the ocean in May, June, July, and August, 65, 83, 90, and 100%, respectively, showed an ocean growth pattern on their scales. Mean estimated ocean growth rates of cutthroat trout (including fish with and without ocean growth) were 0.47, 0.78, 1.03, and 2.60 mm/day, assuming an ocean entry date of 1 April, 1 May, 10 May, and 31 May, respectively. Since the median date of ocean entry of cutthroat trout smolts is sometime in early May (Giger 1972, Loch and Miller 1988, Dawley et al. 1985), growth rate estimates using 1 May or 10 May as an ocean entry date (0.78 and 1.03 mm/day) are probably closest to the true average growth rate of cutthroat trout in the ocean. Ocean growth rates based on the slope of the geometric mean regression (Ricker 1973) of back-calculated ocean growth and julian date was 1.22 mm/day (n = 101, r = 0.67), fairly close to the mean growth rates of individual fish assuming early May ocean entry dates.

Almost all juvenile steelhead with readable scales were caught in May and June. Only 30% and 50%, respectively, of the steelhead caught in these two months showed signs of ocean growth on their scales. This suggests that the steelhead caught in May and June were, on average, in the coastal ocean for less time than the cutthroat trout caught in the same months, either because of later ocean entry or rapid migration of steelhead out of coastal waters. Back-calculated ocean growth rates of juvenile steelhead (including fish with and without ocean growth) were 0.21, 0.32, and 1.06 mm/day for assumed ocean entry dates of 15 April, 1 May, and 17 May, respectively. Downstream migration of steelhead smolts in the Columbia River estuary was half completed around the third week in May (Dawley et al. 1985). Consequently, the ocean entry date of 17 May probably gives the best estimate of average growth rate in the ocean (1.06 mm/day). This growth rate was similar to the average growth rate for cutthroat trout using an early May date of ocean entry. The lack of steelhead caught late in the summer precluded estimating mean growth rate from change in back-calculated ocean growth with time.

Food habits

Cutthroat trout Fishes were by far the dominant prey of juvenile cutthroat trout in terms of frequency, number, and weight. Hexagrammids, scorpaenids, northern anchovy *Engraulis mordax*, and the brown Irish lord *Hemilepidotus spinosus* were the dominant fish taxa identified (Appendix Table 1). One unidentified Pacific salmon, *Oncorhynchus* sp. [81 mm total length (TL)], was found in the stomach of a 221-mm cutthroat trout collected 11.4 km off the mouth of the Columbia River in July 1981. Fishes made up more than 75% of the biomass consumed during all years, but they decreased in importance in the diet as the summer progressed, so that by late summer several other prey taxa such as euphausiids, hyperiid amphipods, and decapod larvae were important. Prey fishes found in cutthroat stomachs averaged 52.5 mm TL (SD 21.8) and ranged from 21 to 101 mm. No significant relation ($n = 46$, $r = 0.30$, $p = 0.16$) was found between the lengths of cutthroat trout and their fish prey.

Steelhead The diet of juvenile steelhead trout was more diverse than that of cutthroat trout. Both arthropods and fishes were important prey items. Prey of steelhead trout ranged from small barnacle larvae and copepods to larger juvenile fishes and squids. Euphausiids, mainly *Thysanoessa spinifera* or *Euphausia pacifica*, accounted for over 75% of the total IRI for all years combined (Appendix Table 1). Fishes were more important, however, on a weight basis making up about 60% of the total biomass consumed. Juvenile rockfishes (*Sebastes* spp.), sandlance *Ammodytes hexapterus*, brown Irish lord *Hemilepidotus spinosus*, and greenlings (*Hexagrammos* spp.) were the dominant fish taxa identified. With the exception of barnacle cypris larvae and hyperiid amphipods which were quite numerous in stomachs collected at several stations, all other prey taxa were relatively unimportant. No relationship between predator and fish prey size was found ($n = 38$, $r = 0.19$, $p = 0.25$). However, steelhead, which had a smaller mean length than cutthroat trout, consumed a smaller mean size ($\bar{x}$ 35.9 mm TL, SD 16.6 mm) and size range (7–72 mm) of prey fishes than cutthroat trout.

The relative proportions by weight of the major prey categories varied substantially among the years sampled. Usually, fishes contributed the majority of the weight to the diet, but during the relatively strong upwelling years of 1982 and 1985 (Fisher and Pearcy 1988) euphausiids were more important. The largest number of prey categories occurred in steelhead and cutthroat stomachs during the relatively weak upwelling summers of 1981 and 1984.

The Percent Similarity Index between cutthroat trout and steelhead was 39% for all cruises combined.

Discussion

Cutthroat and steelhead trout have evolved contrasting migratory behavior in the ocean. Both species were absent in purse seine catches during September of their first summer in the ocean (Miller et al. 1983, Loch and Miller 1988; this paper), apparently because they migrated out of the coastal ocean. Cutthroat return to estuaries and freshwater streams from mid- to late summer (Giger 1972, Loch 1982), whereas most steelhead migrate far offshore during their first summer in the ocean (Hartt and Dell 1986).

Although some aspects of the life histories of cutthroat and steelhead trout are similar, their ecologies in marine waters differ. Steelhead commonly spend 2–3 years in the ocean and attain a large size before initiating their spawning migrations to freshwater. Some, however, return after only one full year in the ocean, and some return, though usually do not spawn, after several months in the ocean (Everest 1973). Apparently anadromous cutthroat trout return to freshwater after only a few months in coastal waters and rarely overwinter at sea. Giger (1972) did not identify any coastal cutthroat that had overwintered in the ocean, based on analyses of circuli patterns from scales of fish returning to coastal rivers of Oregon. Fish that migrated to sea in the spring invariably returned to freshwater in the summer or fall of the same year. Similarly, Armstrong (1971), Jones (1982) and Loch, and Miller (1988) did not report any cutthroat that spent an entire year in the ocean. J. Johnston (Wash. Dep. Wildl., Olympia, pers commun. 8 March 1990) found a few cutthroat trout in Hood Canal, WA, during February and March, fish that evidently overwintered in marine waters. Most cutthroat spawn after their return to freshwater, but according to Johnston (1982) a large percentage of the Columbia River, Puget Sound, British Columbia, and Alaska stocks of cutthroat overwinter but do not spawn in freshwater after their first summer in the ocean. Jones (1977) reported that less than 50% of the cutthroat migrating into Petersburg Creek in southeast Alaska were approaching sexual maturity. In some instances, coastal cutthroat may migrate downstream but not into the ocean. Smolts from the Cowlitz River in Washington may remain in the Columbia River estuary for a year (Tipping 1981 as cited by Johnston 1982), and some adults that return to spawn in Sand Creek, OR, and Prairie Creek, CA, had no ocean growth on their scales (Sumner 1972, DeWitt 1954). Tomasson (1978) thought that coastal cutthroat did not migrate in large numbers beyond the Rogue River estuary.

Because coastal cutthroat only spend several months in the ocean, it is assumed that they inhabit waters close to the coast and not far from their homestream (Giger 1972). Johnston (1982) observed that anadromous cutthroat usually frequented waters less than 3 meters in depth in Puget Sound and that migration of tagged wild cutthroat did not extend much beyond 50 km from the home stream. However, cutthroat were caught by Loch and Miller (1988) up to 31.5 km offshore and within the Columbia River plume between Tillamook Bay, OR, and Willapa Bay, WA, suggesting more extensive offshore movements. Sumner (1972) also thought that cutthroat originating from the Columbia River basin may traverse along the coast within the Columbia River plume. Our data also suggest that some cutthroat undertake substantial movements along the coast (>250 km) and are found as far offshore (37–46 km) as the more oceanic steelhead smolts during the summer. One fish was caught 66 km offshore. Thus some individuals may reside far offshore along an open coast, as opposed to staying close to shore as they presumably do in protected inlets like Puget Sound (Johnston 1982). Straying of returning sea-run hatchery cutthroat trout is common (Bulkley 1966, Giger 1972, Jones 1977). Giger (1972) reported straying of marked hatchery cutthroat between the Nestucca, Siuslaw, and Alsea Rivers of the central Oregon coast. Most of the strays were recovered in rivers south of the river of release, possibly the result of advection by coastal currents during the early summer period of ocean residence, similar to that seen for coho salmon (Pearcy and Fisher 1988).

Giger (1972) noted a non-random distribution in the number of cutthroat smolts and kelts in seine samples in the Alsea estuary during the spring and "large schools" of sea-run fish in estuaries in the fall. He thought that anadromous cutthroat trout formed schools while at sea. However, we found no evidence of schooling from our limited ocean catches. Most cutthroat were caught singly. To our knowledge, schooling of cutthroat or steelhead trout in the ocean has not been documented.

Steelhead migrate long distances into oceanic waters and are widely distributed in the North Pacific Ocean based on catches of marked and unmarked fish (Sutherland 1973; Pearcy and Masuda 1982, 1987; Okazaki 1983; Hartt and Dell 1986; Light et al. 1988). Miller et al. (1983) found that juvenile steelhead caught in purse seines between Tillamook Bay and Willapa Bay occurred farther offshore than juvenile coho or chinook salmon and migrated out of the coastal sampling area early in the summer. Purse seining and tagging studies by Hartt and Dell (1986) from Cape Flattery, WA, to the Aleutian Islands clearly showed that juvenile steelhead migrate directly offshore rather than along a coastal belt where other juvenile salmonids typically migrate. Recovery of steelhead during their first summer in the ocean in the Gulf of Alaska confirms rapid migrations of some fish into oceanic waters far from land. Pearcy and Masuda (1982) report on a steelhead captured over 1600 km from land only a few months after its initial ocean entry.

These conclusions of immediate migrations of steelhead offshore and into subarctic waters of the North Pacific after ocean entry, and residence in oceanic waters during their first winter in the ocean, do not apply to all steelhead. Most steelhead from the Rogue River in Oregon (the "half-pounder" runs) return to freshwater after only a few months following their initial migration to the ocean (Everest 1973), and likely do not migrate very far in the ocean. The recovery of marked Rogue River summer steelhead south of the Rogue River (Everest 1973), and the rarity of marked steelhead originating from streams south of Cape Blanco in waters to the north of Cape Blanco in our catches, suggest that these steelhead from the southern extremity of their range may not migrate to the north after ocean entry. This conclusion is supported by the high seas distribution of tagged steelhead. Although 9 tagged steelhead from California and 11 from Oregon streams have been recovered north of 45°N in the northeastern Pacific, only 3 fish with coded-wire tags from California have been recovered at sea of the over 1 million coded-wire tagged steelhead released between 1980 and 1985, and only one was caught north of California (Light et al. 1988, Pacific States Marine Fisheries Comm. unpubl.). Possibly southern steelhead reside in the strong upwelling zone off northern California and southern Oregon (Bakun 1975).

The feeding habits of juvenile steelhead and cutthroat trout in estuaries and in coastal waters are similar. Both species feed intensively on gammarid amphipods and insects in estuaries on their initial migration to the sea, but steelhead smolts also eat the benthic mollusk *Corbicula* (Loch 1982, McCabe et al. 1983, Bottom et al. 1984). During their early residence in waters along the open coast, cutthroat trout feed primarily on fishes (Armstrong 1971, Fresh et al. 1981, Brodeur et al. 1987a, Loch and Miller 1988, this paper). We found that steelhead trout also consumed fish but had a more varied diet than cutthroat trout. Euphausiids and other crustaceans were important in the diet of steelhead trout, especially during the strong upwelling years of our study when euphausiids may have been abundant (Brodeur 1986). Many prey species identified in the diets of the trout species (juvenile rockfishes, hexagrammids, anchovy, *Cancer* spp. megalopae, and insects) are commonly found in the neustonic layer (Brodeur et al. 1987b, Shenker 1988) which suggests that these trouts feed in surface waters. The occurrence of a juvenile salmon in the diet of juvenile cutthroat is noteworthy since larger individuals (>300 mm) of this species were identified as one of the few fish predators on juvenile salmonids among the 20 species of nekton examined from these same purse seine catches (Brodeur et al. 1987a).

Dietary overlap of 39% between cutthroat and steelhead trout based on percent similarity was higher than the overlap values between these species of trout and the juveniles of four species of salmon caught in purse seines, with two exceptions. The highest overlap values were between cutthroat trout and juvenile chinook salmon (49%) because of the common utilization of fishes in the diet, and between juvenile steelhead trout and juvenile sockeye salmon (43%) because of the common occurrence of euphausiids.

The average growth rate of cutthroat trout in the ocean based on our scale analysis was 0.8 and 1.0 mm/day (based on 1 May and 10 May dates of ocean entry, respectively) and 1.2 mm/day (based on change in back-calculated ocean growth with time). These estimates are similar to the growth rates of about 1.0 mm/day for age 2. wild cutthroat and 0.9 mm/day for hatchery cutthroat, assuming a 3-month ocean residence (Giger 1972) and 0.7–0.8 mm/day for fish after their first 5–6 months in the ocean (Sumner 1962). Johnston (1982) reported an average growth rate of 1.0 mm/day during the time spent at sea for cutthroat trout stocks from the Columbia River, coastal rivers, and Puget Sound rivers. Our average growth rate for steelhead of 1.1 mm/day (based on a 17 May date of ocean entrance) is similar to that for cutthroat trout. It is about the same as the average ocean growth of 1.3 mm/day calculated by Everest (1973), the 0.8 mm/day estimated by K. Kenaston (Oreg. Dep. Fish Wildl., Corvallis, pers. commun. 16 June 1989) for summer-run steelhead "half-pounders" of the Rogue River, and the 1.5 mm/day estimated for first-year ocean growth of steelhead from Vancouver Island (Hooten et al. 1987). Data on ocean growth of steelhead during their first year in the ocean is also provided by recovery of fish with coded-wire tags. These include growth rates of about 1.0 mm/day for a fish caught in the Gulf of Alaska, based on the mean size of the same tag code of steelhead smolts when caught about 60 days earlier in the Columbia River (Pearcy and Masuda 1982), and growth rates of 0.7, 1.0, and 1.2 mm/day for coded-wire tagged steelhead recovered 198, 186, and 173 days, respectively, after release (Pacific States Marine Fisheries Comm. unpubl.). Lengths at release were estimated from release weight using the length-weight relationships for steelhead smolts given by Everest (1973). The average growth rate of steelhead during their first full year in the ocean was about 1.0 mm/day for fish returning to California streams (calculated from data in Shapovalov and Taft 1954), 0.6 mm/day for fish caught on the high seas (Sutherland 1973), and 0.85 mm/day for fish from the Keogh River, British Columbia (Ward and Slaney 1988). These estimates suggest fairly similar growth rates for both cutthroat and steelhead trout during early ocean life. Apparently cutthroat trout are small when they return to spawn because they spend less time in the ocean, not because of an inherently lower growth rate.

If coastal cutthroat trout have the potential for a large increase in size during ocean life, why do they curtail marine growth by returning to freshwater each winter rather than remaining in the ocean for several years like most steelhead trout? We present three hypotheses for the adaptive value of this behavior.

Early maturation of cutthroat trout, after only a few months in the ocean, may have evolved as a response to low survival (Cole 1954), either in the ocean or freshwater, especially if postreproductive survival is low after the age at first breeding (Schaffer 1974). Cutthroat trout do not appear to have distinctly lower ocean survival than steelhead, however, based upon the reports in literature. Giger (1972) states that coastal cutthroat exhibited comparatively high rates of survival during summer periods of ocean residence between spawnings. He estimated ocean survival rates of 20–40% for hatchery cutthroat smolts between release in the spring and return in the fall, and survival rates of 14–39%, 17–35%, and 12–25% between first and second, second and third, and third and fourth spawnings, respectively, based on trap or net catches of fish returning to four Oregon coastal streams. Sumner (1962) estimated that 17–50% of coastal cutthroat trout survived between successive spawnings, and Jones (1978) reported marine survival of 17%. Tomasson (1978), on the other hand, noted that 92% of the fish returning to the Rogue River were first migrants, suggesting low survival of repeat spawners, and Michael (1983, 1989) reported marine survival rates of 2–20% between smolt outmigration and first return to freshwater for coastal cutthroat trout.

Cutthroat survival to an ocean age of 2, the age when many steelhead trout return for their initial spawning (Withler 1966, Shapovalov and Taft 1954, Chapman 1958), is about 5% (assuming 20% survival from smolt to first spawning and 25% survival from first to second spawning, based on Giger's estimates), a value which is close to the average for smolt to adult return for steelhead (Bley and Moring 1988), but less than the mean ocean survival of 16% based on maiden-run fish given by Ward and Slaney (1988). Thus survival rates to ocean age 2 of these two species appear to be roughly similar, as is survival of repeat spawners of cutthroat trout and steelhead trout (Giger 1972, Withler 1966, Ward and Slaney 1988). Lower ocean survival or lower postreproductive survival of cutthroat trout than steelhead may not be a cogent explanation for cutthroat trout spawning at an early age and small size.

The second hypothesis is that small size at maturity in cutthroat trout relative to steelhead trout may have evolved as a result of the distance and rigor of spawning migrations. Schaffer and Elson (1975) concluded that the mean age of first spawning of Atlantic salmon increased with the difficulty of upstream migration, as estimated by the distance ascended into freshwater. Coastal cutthroat rarely penetrate inland more than 160 km (Johnston 1982), and hence may not need the swimming performance or energy reserves required for the long and arduous upstream migrations that some steelhead undertake at the time of maturity.

Finally, the small size at maturity attained by cutthroat trout may permit utilization of small, shallow tributaries for spawning and rearing where interspecific competition with other anadromous salmonids is reduced. Small streams are known to be important spawning and rearing areas of cutthroat trout (DeWitt 1954, Needham and Gard 1959, Lowry 1965, Johnston 1982, Trotter 1989). Sea-run cutthroat trout generally spawn in tributaries with a lower velocity and shallower depth than steelhead (Hunter 1973). Hartman and Gill (1968) reported that where both anadromous cutthroat trout and steelhead were sympatric, juvenile cutthroat were predominant in headwater tributaries and steelhead in larger river reaches. Cutthroat trout are behaviorally subordinate to steelhead and coho salmon in agonistic encounters (Nilsson and Northcote 1981, Glova 1986, Griffith 1988) and their populations appear to be suppressed by competition from anadromous salmonids (R. House, Unpubl.). The lack of morphological specialization of cutthroat trout to either fast or slow water may be another reason why this species is dominated by coho salmon and steelhead in areas of sympatry (Bisson et al. 1988). Anadromous cutthroat are known to penetrate, spawn, and rear farther into a watershed than steelhead trout (Michael 1983), sometimes above natural falls or log jams (Mitchell 1988; R. House, Unpubl.) that were considered to be barriers to anadromous salmonids (see Michael 1983). Therefore, small size at maturity may be adaptive by allowing anadromous cutthroat trout to spawn and rear in numerous small tributaries of coastal streams where other salmonids are absent or less abundant.

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Appendix Table 1

Percent frequency occurrence (F), percent number (N), percent weight (W), and percent index of relative importance (IRI) of food items in juvenile steelhead and cutthroat trout stomachs for all years combined. Values in parentheses are summaries by major taxonomic categories.

	Steelhead trout				Cutthroat trout			
Prey taxa	F	N	W	IRI	F	N	W	IRI
Cnidaria								
Velella velella	1.1	<0.1	0.1	<0.1	—	—	—	—
Siphonophora								
Unidentified	1.1	<0.1	<0.1	<0.1	—	—	—	—
Annelida								
Tomopteris septentrionalis	1.1	<0.1	<0.1	<0.1	—	—	—	—
Tomopteris spp.	1.1	<0.1	<0.1	<0.1	—	—	—	—
Mollusca								
Gastropoda								
Limacina helicina	1.1	4.8	0.1	0.1	3.2	0.5	0.1	<0.1
Cephalopoda								
Loligo opalescens	1.1	<0.1	<0.1	<0.1	—	—	—	—
Unidentified	1.1	<0.1	0.1	<0.1	—	—	—	—
Arthropoda								
Copepoda	(4.2)	(4.0)	(0.1)					
Neocalanus cristatus	1.1	0.1	<0.1	<0.1	—	—	—	—
Epilabidocera longipedata	1.1	<0.1	<0.1	<0.1	—	—	—	—
Euchaeta elongata	1.1	3.9	<0.1	0.1	—	—	—	—
Unidentified	1.1	<0.1	<0.1	<0.1	—	—	—	—
Cirripedia								
Unidentified cypris	18.1	9.6	0.5	3.4	—	—	—	—
Unidentified remains	6.4	0.4	1.1	0.2	—	—	—	—
Isopoda								
Gnorimosphaeroma oregonensis	1.1	0.1	<0.1	<0.1	—	—	—	—
Idotea fewkesi	—	—	—	—	1.6	<0.1	0.1	<0.1
Amphipoda	(29.5)	(5.1)	(1.6)					
Caliopius laeviusculus	1.1	<0.1	<0.1	<0.1	—	—	—	—
Unidentified Gammaridea	1.1	<0.1	<0.1	<0.1	—	—	—	—
Hyperia medusarum	3.2	0.1	0.3	<0.1	—	—	—	—
Hyperoche medusarum	21.3	2.2	1.0	1.3	6.5	0.7	0.1	0.1
Themisto pacifica	3.2	2.7	<0.1	<0.1	1.6	<0.1	0.1	<0.1
Brachyscelus crusculum	1.1	<0.1	0.1	<0.1	—	—	—	—
Unidentified Hyperiidea	2.1	0.1	0.1	<0.1	1.6	0.2	<0.1	<0.1
Caprella incisa	1.1	<0.1	<0.1	<0.1	—	—	—	—
Euphausiacea	(67.4)	(54.1)	(32.7)		(24.2)	(16.0)	(2.0)	
Euphausia pacifica	43.6	8.3	12.0	16.4	8.1	0.5	0.4	0.2
Nematoscelis difficilis	—	—	—	—	1.6	0.1	0.1	<0.1
Thysanoessa spinifera	50.0	43.9	19.8	58.8	9.7	9.4	0.2	2.4
Thysanoessa longipes	1.1	1.3	<0.1	<0.1	—	—	—	—
Nyctiphanes simplex	1.1	0.1	<0.1	<0.1	—	—	—	—
Unidentified furcilia	1.1	<0.1	<0.1	<0.1	—	—	—	—
Unidentified	12.8	0.5	0.9	0.3	8.1	6.0	1.3	1.5

Appendix Table 1 (continued)

Prey taxa	Steelhead trout F	N	W	IRI	Cutthroat trout F	N	W	IRI
Euphausiacea (continued)								
Decapoda	(14.7)	(5.6)	(1.9)		(17.7)	(4.9)	(1.4)	
Crangon spp. zoea	—	—	—	—	1.6	0.5	<0.1	<0.1
Pagurus spp. zoea	—	—	—	—	1.6	<0.1	<0.1	<0.1
Pagurus spp. megalopae	—	—	—	—	1.6	0.5	<0.1	<0.1
Porcellanidae megalopae	—	—	—	—	1.6	0.5	<0.1	<0.1
Pugettia producta zoea	—	—	—	—	3.2	0.1	<0.1	<0.1
Cancer antennarius megalopae	2.1	<0.1	<0.1	<0.1	1.6	0.1	<0.1	<0.1
Cancer magister megalopae	8.5	0.5	1.4	0.3	12.9	2.9	1.3	1.4
Cancer oregonensis megalopae	5.3	2.4	0.4	0.3	3.2	0.1	<0.1	<0.1
Cancer spp. zoea	2.1	2.7	<0.1	0.1	1.6	<0.1	<0.1	<0.1
Pinnotheridea megalopae	—	—	—	—	1.6	<0.1	<0.1	<0.1
Unidentified larvae	1.1	<0.1	<0.1	<0.1	1.6	<0.1	<0.1	<0.1
Insecta	(8.4)	(0.2)	(0.2)		(8.1)	(1.2)	(0.8)	
Choristoneura occidentalis	1.1	<0.1	<0.1	<0.1	—	—	—	—
Hymenoptera	—	—	—	—	3.2	0.7	0.6	0.1
Coleoptera	1.1	<0.1	<0.1	<0.1	—	—	—	—
Hemerobiidae	1.1	<0.1	<0.1	<0.1	—	—	—	—
Diptera	2.1	<0.1	<0.1	<0.1	1.6	<0.1	<0.1	<0.1
Unidentified	5.3	0.1	0.1	<0.1	6.4	0.5	0.2	0.1
Chordata								
Osteichthyes	(70.5)	(16.0)	(61.4)		(87.1)	(76.2)	(95.1)	
Clupea harengus pallasi	4.2	0.1	2.4	0.2	—	—	—	—
Engraulis mordax	—	—	—	—	9.7	1.3	7.8	2.3
Allosmerus elongatus	1.1	0.1	3.7	0.1	—	—	—	—
Spirinchus thaleichthys	—	—	—	—	1.6	0.1	3.7	0.2
Osmeridae	1.1	<0.1	0.1	<0.1	3.2	0.1	6.6	0.6
Oncorhynchus sp.	—	—	—	—	1.6	0.1	2.0	0.1
Sebastes flavidus	—	—	—	—	1.6	0.1	1.4	0.1
Sebastes jordani	1.1	<0.1	1.2	<0.1	—	—	—	—
Sebastes spp.	21.3	0.4	22.5	9.0	11.3	5.0	7.9	3.8
Anoplopoma fimbria	2.1	0.1	0.1	<0.1	1.6	<0.1	0.9	<0.1
Hexagrammos decagrammus	2.1	0.1	1.8	0.1	9.7	0.7	16.7	4.3
Hexagrammos spp.	4.3	0.1	4.9	0.4	8.1	27.7	7.6	7.3
Ophiodon elongatus	3.2	<0.1	0.9	0.1	3.2	0.1	0.9	0.1
Agonidae	1.1	1.3	<0.1	<0.1	—	—	—	—
Hemilepidotus spinosus	7.4	0.2	4.3	0.6	12.9	0.9	7.4	2.7
Scorpaenichthys marmoratus	3.2	0.1	0.1	<0.1	4.8	4.8	5.2	1.2
Cottidae	3.2	5.3	0.1	0.3	—	—	—	—
Ammodytes hexapterus	10.6	1.6	3.3	1.0	9.7	0.6	2.9	0.9
Ronquilus jordani	1.1	1.3	0.1	<0.1	—	—	—	—
Citharichthys sordidus	1.1	<0.1	0.4	<0.1	—	—	—	—
Psettichthys melanostictus	1.1	0.1	0.8	<0.1	—	—	—	—
Unidentified larvae	13.8	0.5	2.4	0.7	4.8	0.3	0.5	0.1
Unidentified juveniles	8.5	1.5	4.4	0.9	16.1	0.8	10.6	4.7
Unidentified remains	24.5	3.1	7.9	5.0	54.8	33.6	13.0	65.6
Plant material	2.1	<0.1	0.1	<0.1	1.6	<0.1	0.5	<0.1
Number of stomachs examined		98				67		
Number of empty stomachs		4				5		
Mean fork length (mm)		213.4				254.5		
Fork length range (mm)		158–294				162–298		