American Fisheries Society Symposium 57:000–000, 2007
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Comparisons of the Coastal Distributions and Abundances of Juvenile Pacific Salmon from Central California to the Northern Gulf of Alaska

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Abstract.—In this chapter, we describe the distributions and abundances of juvenile Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, chum salmon *O. keta*, pink salmon *O. gorbuscha*, and sockeye salmon *O. nerka* in six regions along the west coast of North America from central California to the northern Gulf of Alaska during the early summer (June and July) and late summer–fall (August–November) of 2000, 2002, and 2004. We also describe fish abundance in relation to bottom depth and to the average temperature and salinity of the upper water column. Salmon were collected in rope trawls from the upper 15–20 m over the open coastal shelf. Catch per unit effort was standardized across the different regions. Subyearling Chinook salmon were found only from central California to British Columbia. Yearling Chinook salmon were widespread, but were most abundant between Oregon and Vancouver Island. Juvenile coho salmon were widespread from northern California to the northern Gulf of Alaska, whereas chum, sockeye, and pink salmon were only abundant from Vancouver Island north into the Gulf of Alaska. Generally, the juveniles of the different salmon species were most abundant at, or north of, the latitudes at which the adults spawn. Abundances were particularly high near major exit corridors for fish migrating from freshwater or protected marine waters onto the open shelf. Seasonal latitudinal shifts in abundance of the juvenile salmon were generally consistent with the counterclockwise migration model of Hartt and Dell (1986). Subyearling Chinook salmon were associated with the high salinity environment found off California and Oregon, whereas chum, sockeye, and pink salmon were associated with the lower salinity environment in the Gulf of Alaska. However, within regions, evidence for strong temperature or salinity preferences among the different species was lacking. Subyearling Chinook salmon were most abundant in shallow, nearshore water.

Introduction

Since the late 1990s, research on the early ocean life of juvenile Pacific salmon *Oncorhynchus* spp. has been conducted in six regions along the west coast of North America, from the Gulf of the Farallones off the central California coast (MacFarlane and Norton 2002) to the area off the Kenai Peninsula in the northern Gulf of Alaska (Weingartner et al. 2002; Boldt and Haldorson 2004) (Figure 1). These concurrent research projects present a unique opportunity for comparing the early ocean ecology of different species of juvenile salmon during their first summer and fall at sea along much of the west coast of North America. Not since the work of Hartt and Dell (1986), which was based on data collected four to five decades ago, has an opportunity arisen to compare juvenile salmon distributions over such a broad area of the northeast Pacific Ocean. The recent research includes sampling off the Washington, Oregon, and California coast, well to the south of the areas sampled by Hartt and Dell (1986).

Variable mortality of juvenile salmon during their first summer and fall in the ocean may exert a dominant influence on year-class success (Fisher and Pearcy 1988; Pearcy 1992; Logerwell et al. 2003; Wertheimer and Thrower 2007, this volume). To understand the vari-

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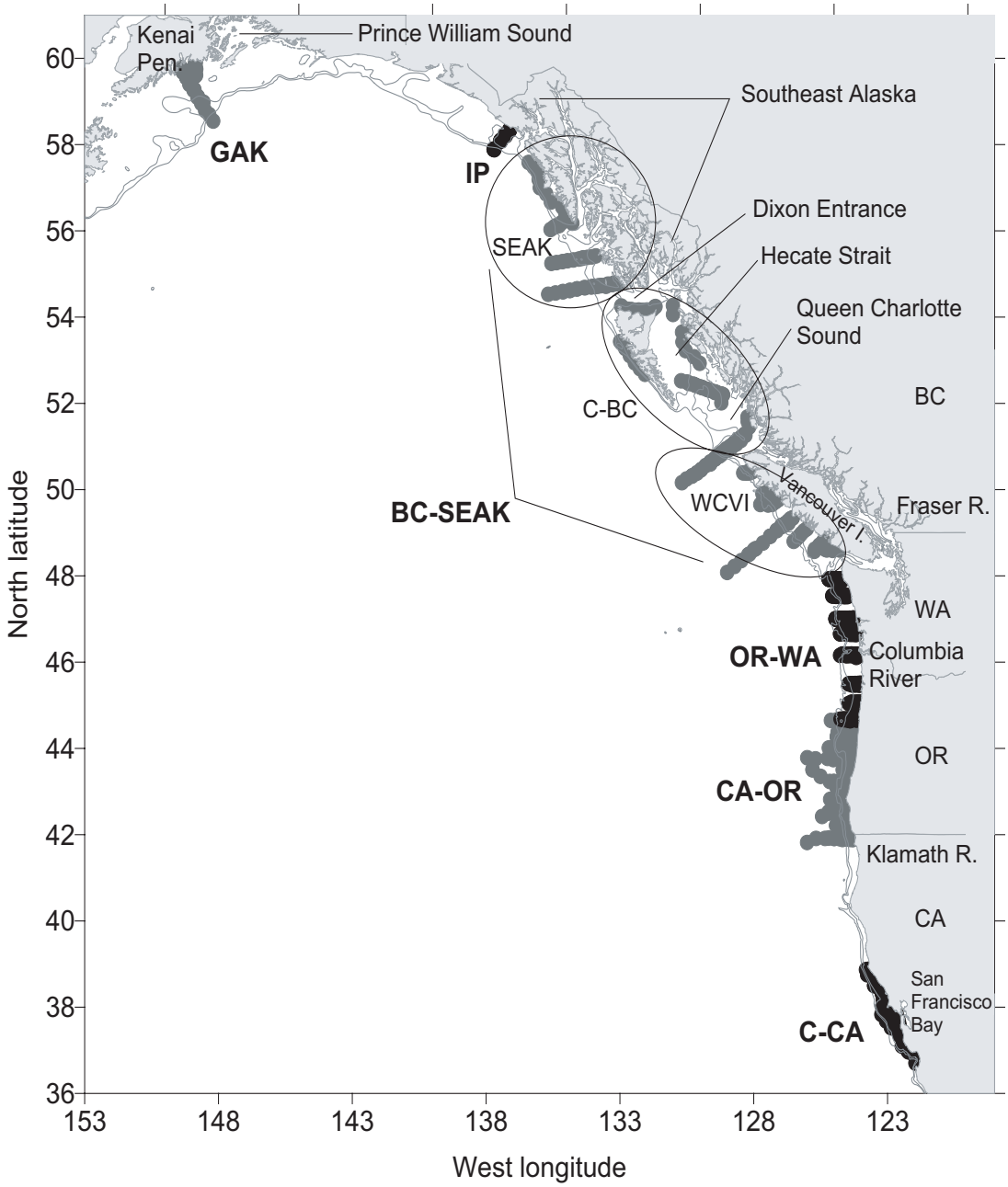


Figure 1. Salmon trawl station locations along the open coastal shelf and slope in the six regions included in this study. The BC-SEAK region was further divided into three subregions (WCVI, C_BC, and SEAK) for some analyses. The 200-m and 500-m isobaths, marking the edge of the continental shelf, are indicated.

ous environmental processes that contribute to mortality of juvenile salmon in the ocean, we need to know their seasonal distribution patterns and the temporally and spatially changing abiotic and biotic environments that each species experiences during their early ocean life.

In this paper, we describe latitudinal and seasonal variations in the abundances of juvenile Chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, chum salmon *O. keta*, pink salmon *O. gorbuscha*, and sockeye salmon *O. nerka* from central California to the northern Gulf of Alaska, using data collected from June through November 2000, 2002, and 2004. The coastal distributions of juveniles of the different salmon species are discussed in relation to the distributions of the adult spawning populations. Seasonal shifts in abundance of the different species are discussed in relation to the counterclockwise migration model for juvenile salmon proposed by Hartt and Dell (1986).

We describe species-specific distribution and abundance patterns in relation to bottom depth and to the temperature and salinity of the upper water column where the juvenile salmon reside. Physical and chemical characteristics of the environment, such as temperature and salinity, play an important role in regulating physiological processes in fish, including osmoregulation, metabolic rates, and growth (Brett 1979; Davis et al. 1998; Walker et al. 2000) and may thus affect juvenile salmon distribution. Along the open coastal shelf of the study area, juvenile salmon are exposed to different environments depending on where and when they enter the ocean and which migration route is used. The study area encompasses a wide range of physical environmental conditions produced by a variety of oceanographic processes. Off California, Oregon, Washington, and Vancouver Island, northerly winds in summer promote inshore coastal upwelling of cold, saline, and nutrient-rich water from deeper layers to the surface, which often results in high rates of phytoplankton productivity (Huyer 1983; U.S. GLOBEC 1994). Discharge of freshwater from the Columbia, Fraser, and other rivers can also produce shallow, low salinity plumes at the surface, the size and location of which vary over time. In the northern Gulf of Alaska, summer snow and ice melt and other freshwater sources promote the formation of the low-salinity, westward-flowing, inshore Alaska Coastal Current (Royer 1982; Weingartner et al. 2002). Preferences of the different juvenile salmon species for particular environments may be revealed by higher abundances of fish in salinity, temperature, or depth ranges that are different from the ranges in the sampling effort as a whole.

Methods

Sampling Programs

Juvenile salmon catch data from six research programs were used in this study (Figure 1). The National Marine Fisheries Service (NMFS) Tiburon/Santa Cruz Laboratory sampled an area off central California from the Gulf of the Farallone Islands to Point Arena (hereafter designated C-CA). The area from extreme northern California to central Oregon (hereafter designated CA-OR) was sampled as part of the Northeast Pacific Global Ocean Ecosystems Dynamics Program (Batchelder et al. 2002). The area from central Oregon to northern Washington (hereafter designated OR-WA) was sampled by the NMFS Northwest Fisheries Science Center and Oregon State University as part of a study of the influence of the Columbia River plume on juvenile salmon distribution, survival and growth. The area off the west coast of Vancouver Island and north into southeast Alaska (hereafter designated BC-SEAK) was sampled by the Pacific Biological Station, Department of Fisheries and Oceans, Canada. A transect off Icy Point, southeast Alaska (hereafter designated IP) was sampled by the NMFS Auke Bay Laboratory as part of the Southeast Alaska Coastal Monitoring project. Finally, the Seward (or "GAK") and Cape Fairfield transects (hereafter designated GAK) off the Kenai Peninsula just to the west of Prince

William Sound in the northern Gulf of Alaska were sampled by the University of Alaska Fairbanks and the University of Washington, as part of GOA GLOBEC (Weingartner et al. 2002). Because the BC-SEAK region covered such a broad latitudinal range (Figure 1), it was further subdivided into three areas for most analyses: the west coast of Vancouver Island (WCVI), the central British Columbia area north of Vancouver Island, including the Queen Charlotte Sound and Islands, Hecate Strait, and Dixon Entrance (C-BC), and the open coast of southeast Alaska (SEAK).

Several of these programs sampled not only over the open coastal shelf and out over the continental slope, but also in fjords, inlets, and sounds. Since the main purpose of this paper is to examine juvenile salmon abundance during migration along the open shelf, we excluded all sampling from "inside" waters (i.e., fjords, sounds, inlets, narrow straits). We considered the large, relatively open waters of Queen Charlotte Sound, Hecate Strait, and Dixon Entrance in the C-BC area to be open shelf regions, and catch data from these areas were included (Figure 1).

Dates of Sampling

We examined the abundances of juvenile salmon caught between June and early November in the different regions (Table 1). Except when producing distribution maps, data were pooled across the 3 years of sampling (2000, 2002, and 2004) and, depending on the analysis, were also grouped by "early" (June and July) and "late" (August to November) periods, by month, or by the entire June–November period.

Sampling Gear

In five of the six regions, a Nordic 264 rope trawl (Net Systems, Bainbridge Island, Washington) was used to capture juvenile salmon. The headrope was kept within about a meter of the surface by floats, the footrope was pulled down by chain weights, and the trawl mouth was spread apart by a pair of 3.0-m Lite foam filled trawl doors. This net was designed to create a mouth opening 30 m wide by 20 m deep. Measurements of the mouth area of the net while fishing varied, no doubt due to varying towing speed and varying conditions of currents, wind, and sea-state. Krutzikowsky and Emmett (2005) reported a mouth area of about 28 m wide by 12 m deep, whereas Fisher et al.[2], using a different vessel, reported a footrope depth averaging 20 m. Mesh size was graduated from 163 cm in the throat of the trawl near the jib lines to 9 cm in the cod end. To retain catches of small fishes, a 0.8-cm mesh liner approximately 6 m long was sewn into the cod end.

In BC-SEAK, a modified midwater trawl (Cantrawl Nets Ltd., Richmond, British Columbia) was used for the sampling (Welch et al. 2004). This net was similar in construction (graduated meshes with a 0.65-cm mesh liner in the cod end) and mouth area (28 m wide by 16 m deep) to that used in the other five regions. The net was fished with the headrope at the surface, but in rough weather, it was sometimes towed with the headrope 15 m below the surface. There have been no side-by-side comparisons of the fishing efficiency of the two nets used for catching juvenile salmonids.

Almost all tows were made during daylight hours, except in the BC-SEAK region, where tows occurred both during the day and the night. Duration of tows varied, but most tows were between 14 and 40 min long.

Standardization of Effort

In order to compare the distribution and abundance of juvenile salmon in the differ-

[2] Fisher, J. P., C. A. Morgan, and C. A. Bucher. 2006. Cruise Report, NWFSC/NMFS, *F/V Predator,* Cruise 05–04, 21 – 30 September, 2005.

Table 1. Ranges in latitude and dates of sampling for juvenile salmon in the six major regions (see Figure 1). For some comparisons of salmon abundance between regions, sampling was divided into "early" (June and July) and "late" (August–October/November) periods.

		Year					
		2000		2002		2004	
Region	Latitude	Early	Late	Early	Late	Early	Late
C-CA	36.78°N–38.88°N	6/20–30	9/26–10/06	6/19–27	9/17–26	7/26–30	10/03–07
CA-OR	41.82°N–44.69°N	5/29–6/11	7/29 – 8/12	6/01–18	8/01–17	–	–
OR-WA	44.64°N–47.94°N	6/17–25	9/19–24	6/21–28	9/26–10/03	6/22–29	9/22–29
BC-SEAK	48.08°N–57.59°N	6/30–7/06	10/04–28	–	10/18–31	6/13–19	10/20– 11/13
IP	57.88°N–58.35°N	6/27, 7/24	8/28, 9/26	6/23, 7/29–30	8/25–26	6/21, 7/24	8/23
GAK	58.54°N–59.91°N	–	–	7/20–26	8/22–24, 10/03–04	7/19–24	8/17–22, 9/12–17

ent regions, effort was standardized. Since the mouth areas of the two nets were similar, the only adjustment was to adjust the catch to a common distance towed. Catch per unit effort (CPUE) was defined as the number of juvenile salmon caught per tow length of 1.5 nautical miles (2.78 km) using the formula [(number caught)/tow duration (h)/tow speed (nautical miles/h)] *1.5 nautical miles. Speed through the water, when available from Doppler, or speed over the ground, calculated from start and end global positioning system positions, was used in calculating distance towed (Table 2).

We could not correct for two factors that have a potential to affect net efficiency. First, the design of the Cantrawl net and the power of the vessels used in the BC-SEAK region allowed for considerably faster towing speeds than could be achieved in the other five regions (Table 2), perhaps increasing the catch efficiency. Second, the efficiency of tows could vary depending on the direction of the tow relative to the direction of swimming of the salmon. For example, Hartt and Dell (1986) found a fivefold increase in catch of juvenile salmon in seines held open to the south compared with catch in seines open to the north. However, we assumed that there was no consistent difference between regions in the average direction of tows that would affect the interregional comparisons of abundance of the juvenile salmon.

The range in CPUE of juvenile salmon in hauls was substantial, from 0 to more than 1,500 fish per standardized towed, and the distribution of CPUE was often very highly and positively skewed. Catch per unit effort in a single tow sometimes accounted for more than half of the total cumulative CPUE for all tows combined within a region and time period. In order to reduce the influence of large catches on the comparisons of juvenile salmon abundance, we $\log_{10}$ transformed the CPUE data for each haul. The $\log_{10}$ transformation compresses the upper end of the distribution, de-emphasizes very large catches, emphasizes order of magnitude differences in abundance (and should also de-emphasize small or moderate differ-

Table 2. Tow speeds used to estimate CPUE (number caught per 1.5 nautical miles tow) in the different regions (see Figure 1). SOG = speed over ground; STW = speed through the water.

Area	Tow speeds used in standardizing catch
C-CA	2000 and 2002: SOG (n = 72, avg. = 3.27 knots, range 2.6–4.0 knots) 2004: STW (n = 52, average = 3.46 knots, range 3.0–3.8 knots)
CA-OR	2000: single estimate of 3.0 knots STW 2002: STW (n = 203, average = 3.23 knots, range 2.9–3.7 knots)
OR-WA	2000: single estimate of 3.4 knots STW (average of STW in other years) 2002 and 2004: STW (n = 135, average = 3.42 knots, range 3.0–4.2 knots)
BC-SEAK	Single estimate of 5.2 knots SOG (n = 493, avg. = 5.19 knots, most tows between 3 and 7 knots SOG)
IP	Single estimate of 2.8 knots SOG
GAK	Single estimate of 2.75 knots SOG (n = 66, average = 2.73 knots, range 1.80–3.51 knots)

ences between regions in average catch efficiency), and helps to make the distributions more symmetrical (Sokal and Rohlf 1995; McCune and Grace 2002). For brevity, the $\log_{10}$(CPUE + 1) values will hereafter simply be called CPUE in the main text.

Distribution Maps

For interested readers, we provide an appenix of 18 figures showing maps of untransformed CPUE by tow for each of the different salmon species and life history types in each region during each month and year of sampling. Although not the main focus of this paper, we thought readers would be interested in seeing the interannual and intraregional variability in abundance and distribution of the juvenile salmon and that these maps might stimulate further research questions.

Regional and Seasonal Trends in Abundance

To investigate latitudinal and seasonal trends in abundance of the different juvenile salmon, the CPUE and percent frequency of occurrence (F.O.) data were pooled across years and grouped by region and by the "early" (June and July) and the "late" (August–November) catch periods. At IP and GAK, more frequent sampling allowed us to examine temporal trends in abundance by month. The F.O. and average, median, and 90th percentile of CPUE were calculated for each salmon species during each sampling period in each region.

Distribution Versus Bottom Depth, Temperature, and Salinity

We examined how the distributions of the different salmon species varied with depth to the bottom and with the average temperature and salinity of the upper 15 m of the water column, the approximate depth to which the net fished. Because the net often fished well into the seasonal thermocline, salmon caught in our nets may have experienced temperatures and salinities very different from those at the surface, depending on their depth distribution. Previous studies indicated that small juvenile coho and Chinook salmon usually are found in the upper 10–20 m (Pearcy and Fisher 1988; Emmett et al. 2004) but that larger juvenile Chinook and coho salmon, about 280 mm fork length (FL) are found to depths of 20–30 m (Orsi and Wertheimer 1995). Therefore, temperature and salinity averaged over a depth range may give a more accurate indication of the

average environment experienced by the juvenile salmon than measurements made at the surface or from the top few meters.

Temperature and salinity at 1-m-depth intervals were obtained from conductivity–temperature–depth casts at each station. Because data from the uppermost meter were often missing, we computed average temperature and salinity from 2 to 15 m depth (14 bins). Data were occasionally missing from other depths in the upper 15 m, so some casts had as few as 10 bins of data.

For each region (years and sampling periods pooled) we examined the distributions of the different salmon species relative to bottom depth, temperature, and salinity by constructing cumulative frequency graphs of salmon abundance (CPUE) versus the physical variables. Hauls were ordered by increasing bottom depth, temperature, or salinity and the cumulative frequency of fish abundance was plotted against the corresponding physical variable. Cumulative frequency of sampling effort (hauls) relative to each physical variable was also shown on the same plots as salmon abundance. The positions and shapes of the salmon abundance and sampling effort plots were examined for differences that could indicate potential habitat preferences of the different fish.

Ages of Juvenile Salmon

In this paper, we defined juveniles as salmon in their first summer or fall of ocean life (i.e., age *x*.0 in the designation of Koo [1962]). The integers before and after the decimal point indicate the winters spent in freshwater and the ocean, respectively. For all but Chinook salmon, juvenile fish could be clearly distinguished from subadult fish (age *x*.1) based on length, since, within time periods and regions, the length modes of the juvenile and subadult fish were well separated (Hartt and Dell 1986; Pearcy and Fisher 1988; Welch et al. 2003, 2004; Trudel et al. 2007a, this volume).

Length–frequency distributions of juvenile Chinook salmon were sometimes multimodal (e.g., Miller et al. 1983; Fisher and Pearcy 1995; Trudel et al. 2007; this volume), mainly as a consequence of a combination of ocean-type (age 0.0), stream-type (age 1.0), and subadult (age *x*.1) fish in the catch (See Discussion). We classified juvenile Chinook salmon as subyearlings (age 0.0) or yearlings (age 1.0) based on the length ranges of marked hatchery fish of known ages collected in the CA-OR and OR-WA regions (J. Fisher and Hinton, NOAA Fisheries, unpublished data; Fisher and Pearcy 1995). Fish ≤ 40 mm FL in June and July or ≤ 50 mm FL from August to November were classified as subyearlings, and fish 141–250 mm FL in June and July or 251–400 mm FL from August to November were classified as yearlings. (In C-CA, in late July, fish ≤ 50 mm FL, 99% of which were ≤ 190 mm FL, were also classified as subyearlings). Larger fish were considered subadults and were not included in any analyses. These classifications are not perfect, mainly because of overlap in lengths of fish of different ages, but we think that they are accurate enough to be useful for showing regional trends in abundance of the two age-classes of Chinook salmon.

Results

Number and Depth Distribution of Hauls

Most sampling occurred over the continental shelf inside of the 500 m isobath (Table 3). Despite a significant effort to sample beyond 500 m in CA-OR, WCVI, SEAK, and IP (Table 3), almost all catches of juvenile salmon occurred inshore of 500 m (Table 4). Therefore, all further analyses include only data collected out to the 500-m isobath.

Table 3. Number of tows for salmon over the continental shelf (≤500-m bottom depth) and over the inner slope (>500 m bottom depth) during the early and late seasons by region (see Figure 1).

	June–July Number of fish hauls		August–November Number of fish hauls	
Region	≤500 m depth	>500 m depth	≤500 m depth	>500 m depth
GAK	22	0	42	1
IP	23	4	13	3
SEAK	11	0	41	16
C-BC	21	0	70	0
WCVI	23	2	49	30
OR-WA	131	6	124	0
CA-OR	169	19	139	39
C-CA	58	0	66	0

Total Catch by Region

Rank order of total catch of the different salmon was pink, chum, sockeye, coho, subyearling Chinook, and yearling Chinook salmon (Table 4). More than 90% of pink, chum, and sockeye salmon were caught from WCVI and north; the largest total catches of these three species occurred in C-BC. No pink or sockeye salmon were caught south of OR-WA, although chum salmon were caught as far south as CA-OR. Coho salmon were caught in all regions from CA-OR and north, but the largest total catches of this species were in OR-WA and WCVI. Yearling Chinook salmon were widespread, occurring in all areas, whereas subyearling Chinook salmon were found only from C-BC south. Off C-CA, only juvenile Chinook salmon were found, 98% of which we classified as subyearling fish (Table 4).

Regional and Seasonal Trends in Abundance

There were clear regional differences in abundance, as measured by CPUE and F.O. (Figure 2). Subyearling Chinook salmon had

Table 4. Total catches of the different life-history types of juvenile salmon over the continental shelf (≤500 m depth) and over the continental slope (in parentheses) in eight areas (see Figure 1) for all sampling periods combined (June–November in 2000, 2002, and 2004). Ages 0.0 and 1.0 are also called subyearlings and yearlings, respectively, in the text.

Region	Chinook salmon age 0.0	Chinook salmon age 1.0	Coho salmon ages 1.0 and 2.0	Chum salmon age 0.0	Sockeye salmon age *x*.0	Pink salmon age 0.0
GAK	0	3	62	455	313	1,509
IP	0	7	54 (3)	358 (2)	65 (5)	555
SEAK	0	9	115	335	197	515
C-BC	8	55	195	4,528	3,813	7,311
WCVI	61 (1)	77 (1)	674	744 (4)	204	323 (8)
OR-WA	764	423	1,070	215 (2)	34	20
CA-OR	215	140	243 (1)	217	0	0
C-CA	879	22	0	0	0	0
All regions	1,927 (1)	726 (1)	2,413 (4)	6,852 (8)	4,626 (5)	10,233 (8)

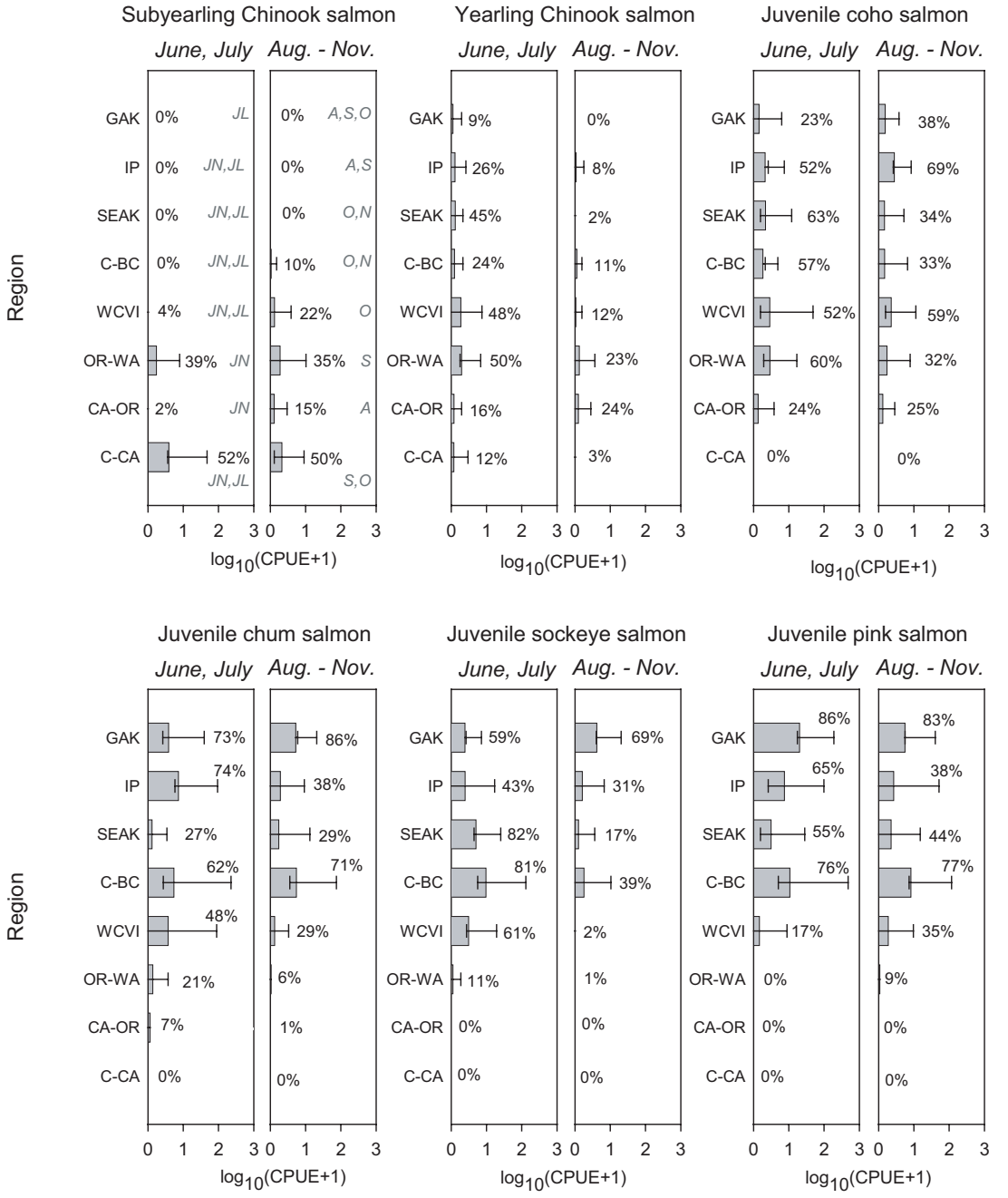


Figure 2. Average (box), median (left whiker), and the 90th percentile (right whisker) of $\log_{10}$(CPUE+1) of the six categories of juvenile salmon by region (see Figure 1) for the early and late sampling seasons. Percent frequencies of occurrence are also indicated. Months sampled within each time period and region are indicated in gray italics in the upper left panels.

the most southerly distribution, whereas pink, sockeye, and chum salmon had the most northerly distributions, and yearling Chinook and coho salmon had the broadest latitudinal range (Figure 2). Coho salmon were widespread and fairly abundant in both seasons, whereas yearling Chinook salmon were only abundant in the early season (Figure 2). Chum, sockeye, and pink salmon were most abundant from the WCVI north to GAK, whereas subyearling Chinook salmon were mainly found from the WCVI south to C-CA. The highest CPUE of either chum, sockeye, or pink salmon was much greater on the whole than the highest CPUE of Chinook and coho salmon (Figure 2). Similarly, the highest F.O. of chum, sockeye, and pink salmon (>80%) was greater than the highest F.O. of coho salmon (69%) or of yearling (50%) or subyearling (52%) Chinook salmon.

Between the two seasons, the distributions of sockeye, chum, coho, and subyearling Chinook salmon shifted northward. This seasonal shift was most evident for sockeye salmon, but was detectable for the other three species as well. Catch per unit effort and F.O. of sockeye salmon decreased greatly between the early and late seasons in all regions except GAK, where it increased (Figure 2). Between seasons, CPUE and F.O. of chum salmon decreased in the southernmost regions (where it occurred from the WCVI and south), increased to the north at SEAK and GAK, remained about the same at C-BC, and decreased at IP (Figure 2). Between the early and late seasons, CPUE of coho salmon decreased moderately in all regions between OR-WA and SEAK in the south, and increased moderately at IP and GAK in the north (Figure 2). Finally, between the early and late seasons, CPUE of subyearling Chinook salmon decreased moderately at C-CA, but increased moderately in all regions to the north where subyearling fish occurred (Figure 2).

Conversely, there was no evidence of northward shifts in abundance of pink salmon or yearling Chinook salmon between the seasons. Between seasons, the abundance of pink salmon decreased moderately in the northern three regions and remained about the same at C-BC, whereas the abundance of yearling Chinook salmon decreased greatly in most regions (Figure 2).

Monthly Abundance Trends at IP and GAK

In the northern Gulf of Alaska, peak CPUE and F.O. of juvenile salmon consistently occurred earlier at IP and later at GAK (Table 5). At IP, CPUE and F.O. of coho salmon increased between June and July and remained relatively high into September, whereas farther north and west at GAK, the highest CPUE and F.O. of coho salmon did not occur until October (Table 5). At IP, both chum and sockeye salmon peaked in abundance in July and were absent by September, whereas at GAK, their abundances peaked in August and remained moderately high into October (Table 5). The temporal pattern of abundance of pink salmon in these two regions was similar to that of chum and sockeye salmon, except that the abundance of pink salmon at GAK was about equally high in both July and August (Table 5).

Regional Differences in Bottom Depth, Temperature, and Salinity

Average bottom depths at tow locations during the two sampling periods were shallowest in the C-CA region (56–62 m) and deepest in the GAK region (200–217 m), varying little between the early and late seasons (Table 6). Average salinity decreased greatly with latitude, from 33.5 to 33.6 practical salinity units (psu) in the south off C-CA, where sampling was mainly inshore and where upwelling of highly saline water was a dominant process (U.S. GLOBEC 1994),

Table 5. Average of $\log_{10}$(CPUE+1) and % frequency of occurrence of juvenile salmon along the IP and GAK transects (≤500-m bottom depth) by month of sampling.

	Region	June	July	August	September	October
Yearling	GAK	–	0.05 (9%)	0.0	0.0	0.0
Chinook	IP	0.08 (20%)	0.13 (31%)	0.0	0.14 (33%)	–
Coho	GAK	–	0.16 (23%)	0.13 (29%)	0.20 (38%)	0.43 (80%)
	IP	0.12 (20%)	0.49 (77%)	0.48 (70%)	0.35 (67%)	–
Chum	GAK	–	0.58 (73%)	0.93 (96%)	0.47 (77%)	0.37 (60%)
	IP	0.23 (40%)	1.35 (100%)	0.37 (50%)	0.0	–
Sockeye	GAK	–	0.39 (59%)	0.77 (79%)	0.46 (62%)	0.28 (40%)
	IP	0.16 (20%)	0.57 (62%)	0.27 (40%)	0.0	–
Pink	GAK	–	1.30 (86%)	1.03 (92%)	0.31 (62%)	0.52 (100%)
	IP	0.08 (20%)	1.49 (100%)	0.56 (50%)	0.0	–

to 29.7–30.7 psu at GAK, where freshwater inputs from rain, rivers, snow and ice melt, and the buoyancy-driven Alaska Coastal Current strongly influenced the upper water column (Royer 1982; Weingartner et al. 2002). Some freshening occurred in the GAK region between the early and late sampling, but in general, latitudinal differences in average salinity were much larger than the temporal differences in average salinity within regions (Table 6). There were no consistent latitudinal or seasonal clines in temperature. Average temperatures were lowest at CA-OR and BC-SEAK and highest at GAK. Changes in average temperatures between early and late seasons were usually less than 1°C (Table 6).

Sampling Effort and Salmon CPUE Relative to Depth, Temperature, and Salinity

Distribution of sampling effort.— Sampling occurred over a fairly narrow range of bottom depths at C-CA, IP, and GAK, but over a much broader range at CA-OR, OR-WA, and BC-SEAK (gray traces in Figure 3). The lowest and highest average water temperatures of the upper water column for the six regions combined were about 8°C and

Table 6. Average bottom depth, and temperature and salinity of the upper water column (2–15 m) during early and late season sampling for juvenile salmon over the continental shelf (≤500 m bottom depth) by region (see Figure 1). Temperature and salinity data were available for most, but not all, trawl stations.

	June–July			August–November		
Region	Mean bottom depth (m)	Mean temp. (°C)	Mean salinity (psu)	Mean bottom depth (m)	Mean temp. (°C)	Mean salinity (psu)
GAK	217	12.8	30.7	200	13.5	29.7
IP	139	11.2	31.8	138	12.5	31.7
BC-SEAK (SEAK, C-BC, WCVI)	132	11.4	31.5	137	10.7	31.7
OR-WA	98	12.3	31.6	93	12.5	32.0
CA-OR	122	10.8	32.4	128	10.2	33.3
C-CA	56	12.2	33.6	62	12.7	33.5

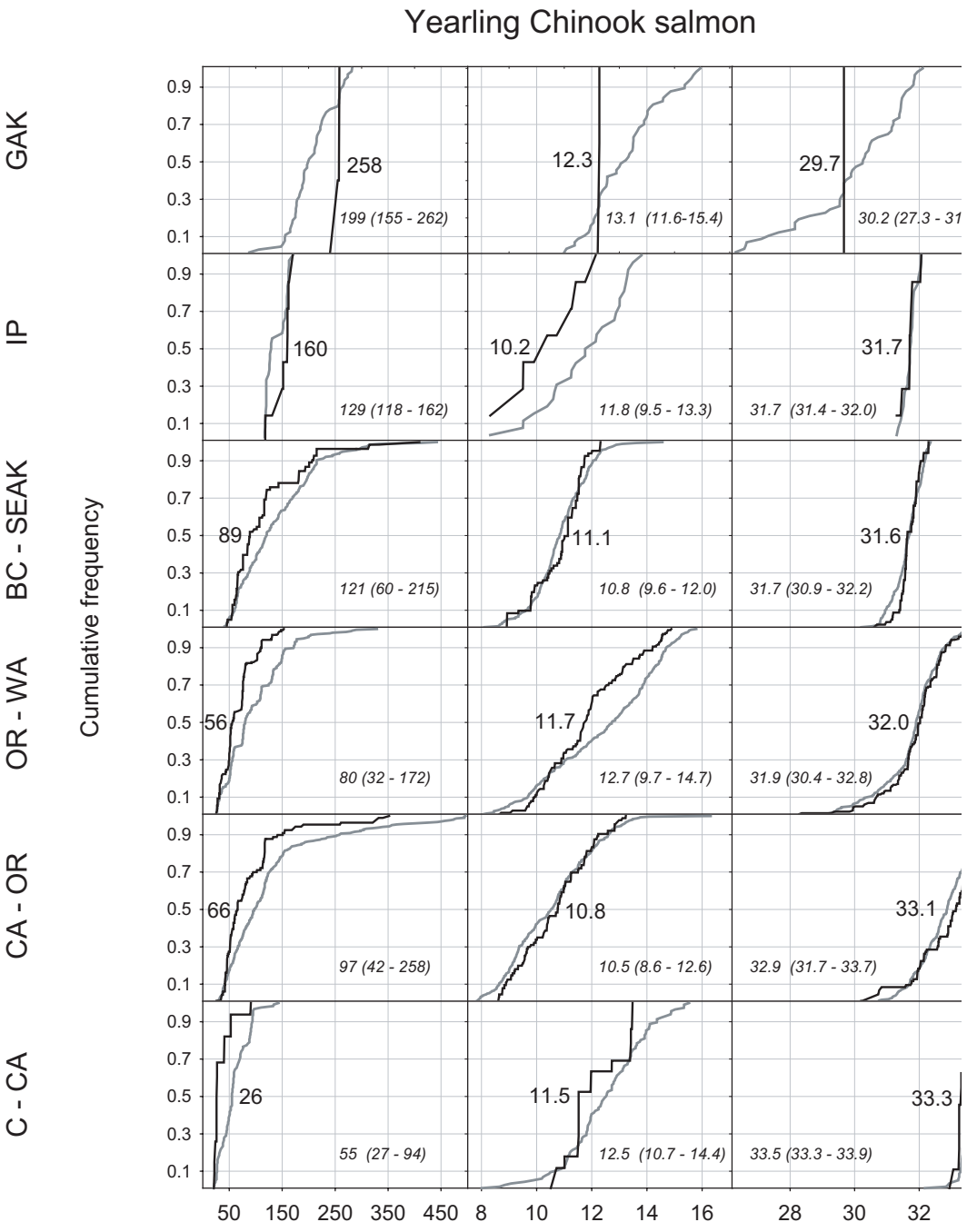


Figure 3. Cumulative frequency distributions of sampling effort (gray lines) and of $\log_{10}$(CPUE+1) of yearling Chinook salmon (black lines) ordered by bottom depth (left), and temperature (center) and salinity (right) of the upper water column (2–15 m) by region (Figure 1) for all months pooled. Shown in small italics are the medians and ranges (10th–90th percentile) of the three environmental variables during sampling. Shown in larger script are the medians of the three environmental variables relative to the cumulative CPUE of salmon.

about 16°C, respectively (Figure 3). Large ranges (as measured from the 10th to 90th percentile) in average temperature occurred in C-CA, CA-OR, and OR-WA (Figure 3), regions where cold, upwelled water was present inshore and warmwater was present offshore or in river plumes. Conversely, the range in temperature in BC-SEAK was fairly narrow. Ranges in salinity were large in the CA-OR, OR-WA, and GAK regions, in the former two regions because of the combination of freshwater discharge from rivers and inshore upwelling of highly saline water and at GAK because of the large amount of freshwater input from snow/ice melt and rain at different times and locations. Range in salinity was considerably narrower in C-CA, where sampling was restricted to the nearshore zone, and also in the BC-SEAK and IP regions (Figure 3).

Distribution of juvenile salmon.—Subyearling Chinook salmon had a shallow, inshore distribution in all regions where they occurred (black traces in Figure 4). Median bottom depths of the distributions of the subyearling fish were remarkably consistent across regions, ranging from 46 to 60 m, and were well inshore of the median depths of sampling, except in C-CA, where all sampling was in relatively shallow water (Figure 4). In contrast to their consistently strong association with depth, subyearling Chinook salmon showed no consistent association with temperature or salinity. For example, in OR-WA, subyearling Chinook salmon were associated with slightly cooler water than was sampled overall, and in CA-OR, they were found mainly in newly upwelled, very saline water, but these patterns were not repeated in the other regions (Figure 4).

Yearling Chinook salmon were distributed in shallower water than was sampled overall from BC-SEAK south to C-CA (Figure 3). They were found in slightly cooler water than was sampled overall in OR-WA and IP but showed no strong salinity preferences within regions (Figure 3). In C-CA, where yearling Chinook were caught infrequently, they were found in very shallow water and were absent from the coldest or warmest water (Figure 3). Yearling Chinook were only caught in a few hauls at GAK (Figure 3).

Coho salmon were slightly more abundant in shallower water than was sampled overall in CA-OR, OR-WA, and BC-SEAK (Figure 5). However, their depth distributions in the IP and GAK regions closely followed the depth distributions of the sampling effort. Most coho salmon were caught over a somewhat narrower temperature range than was sampled overall in the OR-WA and GAK regions, although their temperature distributions followed fairly closely those of the sampling effort in the other regions (Figure 5). The distributions of coho salmon abundance and sampling effort in relationship to salinity were similar in all regions (Figure 5).

Where chum, sockeye, and pink salmon were most abundant (BC-SEAK, IP, and GAK), their distributions followed fairly closely the distributions of sampling effort in relationship to depth, temperature and salinity (Figures 6–8). However, in the BC-SEAK area, sockeye salmon were distributed over slightly deeper water than were chum or pink salmon. In OR-WA, chum, sockeye, and pink salmon were found over a narrower range of temperature and salinity than was sampled overall (Figures 6–8). In CA-OR, chum salmon were caught in relatively few tows and were most abundant in shallower, warmer, and fresher water than was sampled overall (Figure 6).

The Median Depths, Temperatures, and Salinities of the Cumulative Frequency

Distributions of the different juvenile salmon in the different regions are summarized in Table 7. Subyearling Chinook salmon

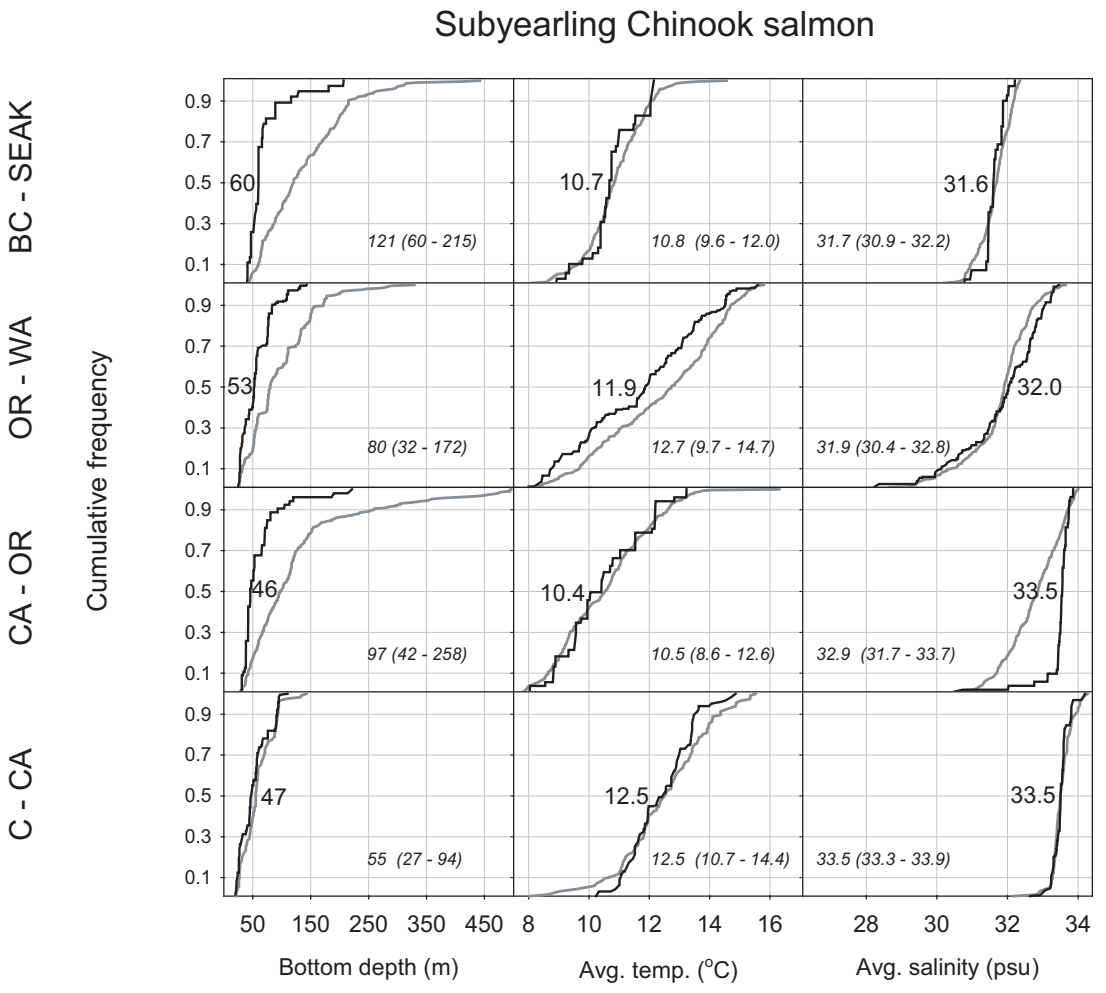


Figure 4. Cumulative frequency distributions of sampling effort (gray lines) and of $\log_{10}$(CPUE+1) of subyearling Chinook salmon (black lines) ordered by bottom depth (left), and temperature (center) and salinity (right) of the upper water column (2–15 m) by region (Figure 1) for all months pooled. Shown in small italics are the medians and ranges (10th–90th percentile) of the three environmental variables during sampling. Shown in larger script are the medians of the three environmental variables relative to the cumulative CPUE of salmon.

were distributed mainly in shallow and often highly saline water, yearling Chinook and coho salmon over a broader range of depths and salinities, and chum, pink, and sockeye salmon in the deeper and relatively dilute waters of the coastal Gulf of Alaska. Large differences in the temperature distributions of the different salmon were not apparent (Table 7).

Discussion

The topics to be addressed include (1) the coastal distributions and abundances of the different juvenile Pacific salmon in relation to the distributions and relative abundances of their parent spawning populations; (2) juvenile salmon distributions on the open shelf in relation to the locations of major

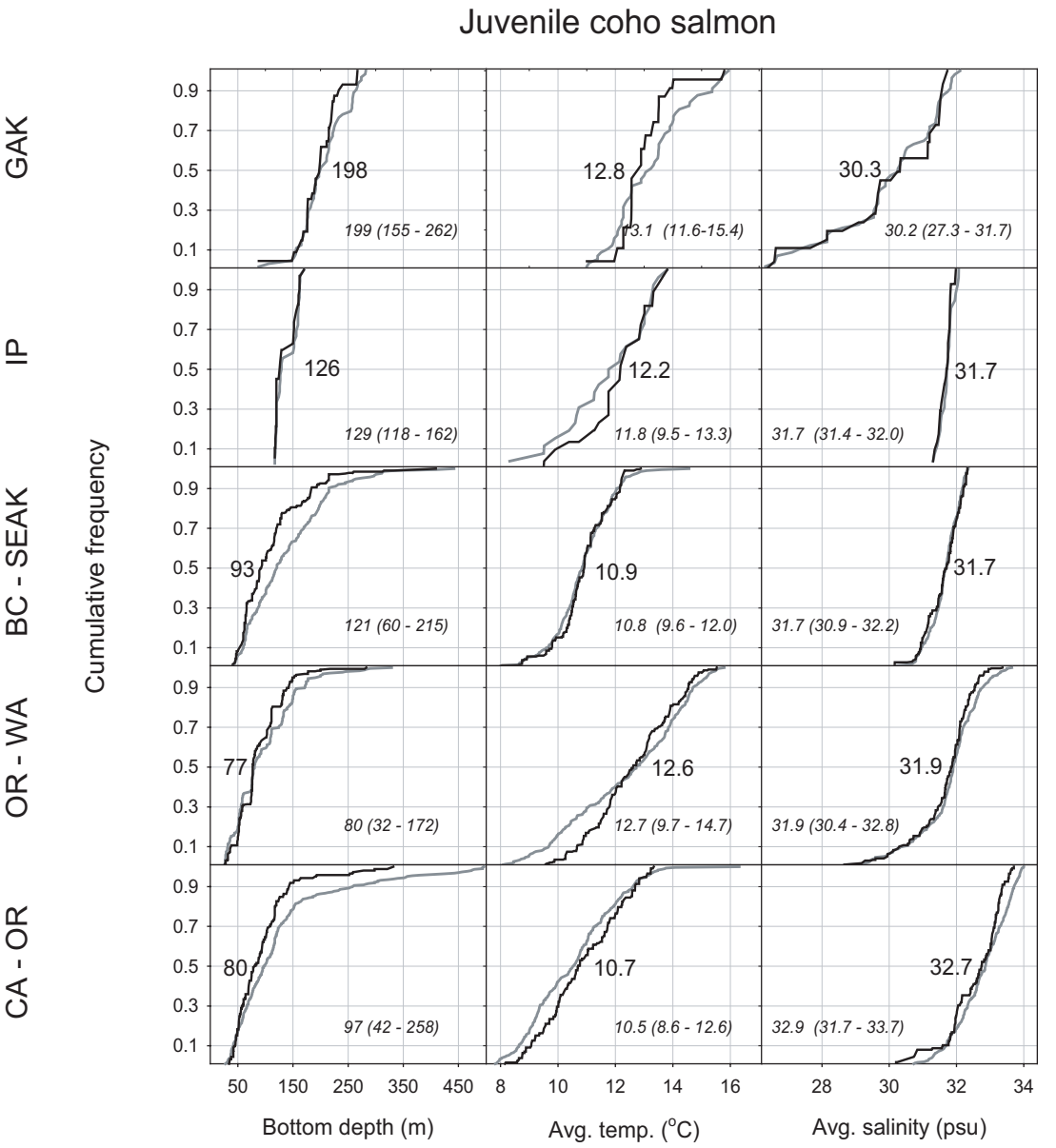


Figure 5. Cumulative frequency distributions of sampling effort (gray lines) and of $\log_{10}$(CPUE+1) of juvenile coho salmon (black lines) ordered by bottom depth (left), and temperature (center) and salinity (right) of the upper water column (2–15 m) by region (Figure 1) for all months pooled. Shown in small italics are the medians and ranges (10th–90th percentile) of the three environmental variables during sampling. Shown in larger script are the medians of the three environmental variables relative to the cumulative CPUE of salmon.

exit points of fish leaving freshwater or protected marine waters and entering the open shelf (i.e., straits, river mouths); (3) temporal changes in the distributions of the different salmon during their first summer and fall in the ocean and whether these changes

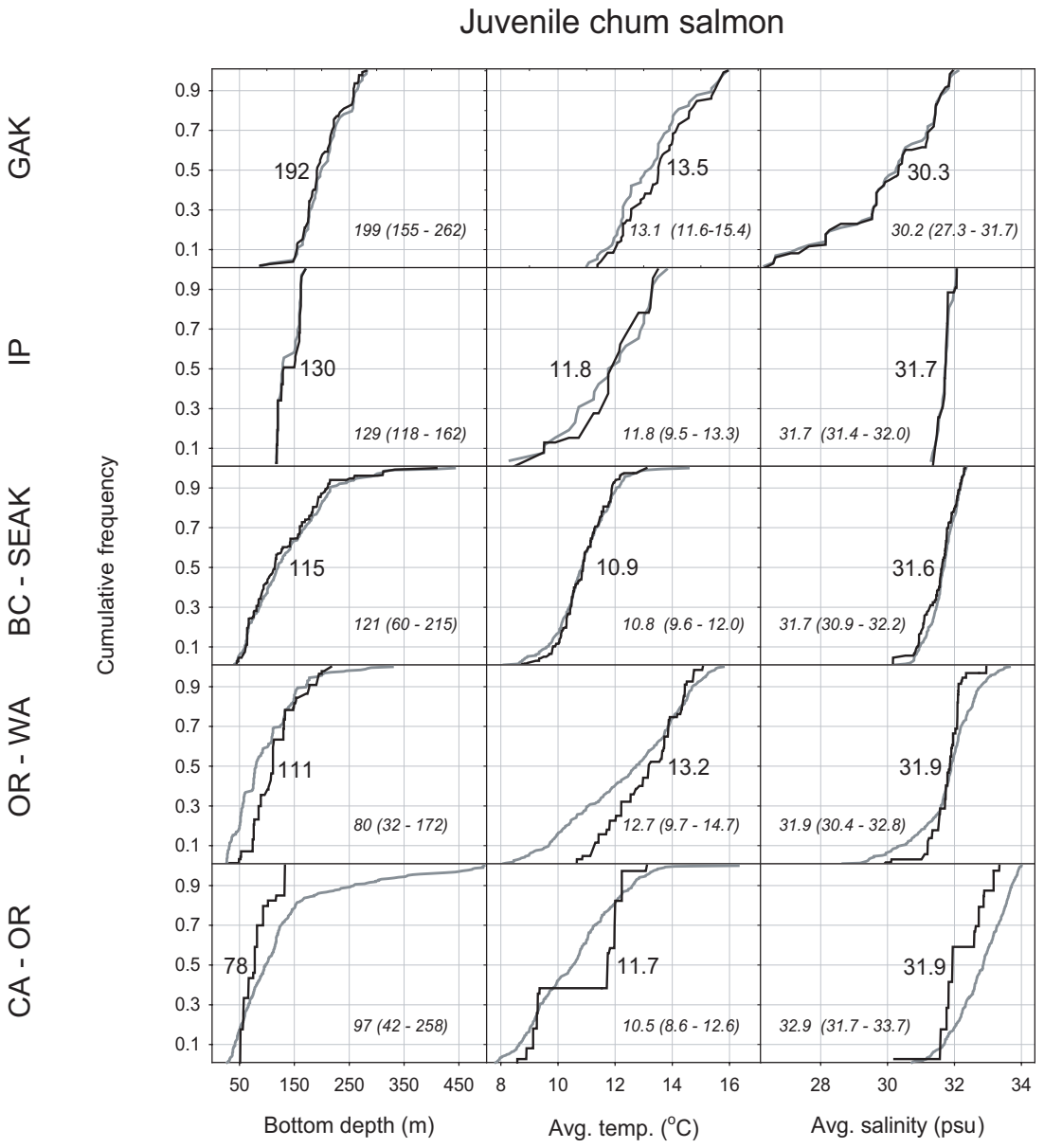


Figure 6. Cumulative frequency distributions of sampling effort (gray lines) and of $\log_{10}$(CPUE+1) of juvenile chum salmon (black lines) ordered by bottom depth (left), and temperature (center) and salinity (right) of the upper water column (2–15 m) by region (Figure 1) for all months pooled. Shown in small italics are the medians and ranges (10th–90th percentile) of the three environmental variables during sampling. Shown in larger script are the medians of the three environmental variables relative to the cumulative CPUE of salmon.

are consistent with the counterclockwise coastal migration model proposed by Hartt and Dell (1986); and (4) the evidence for and against depth, temperature, or salinity preferences among the different juvenile salmon.

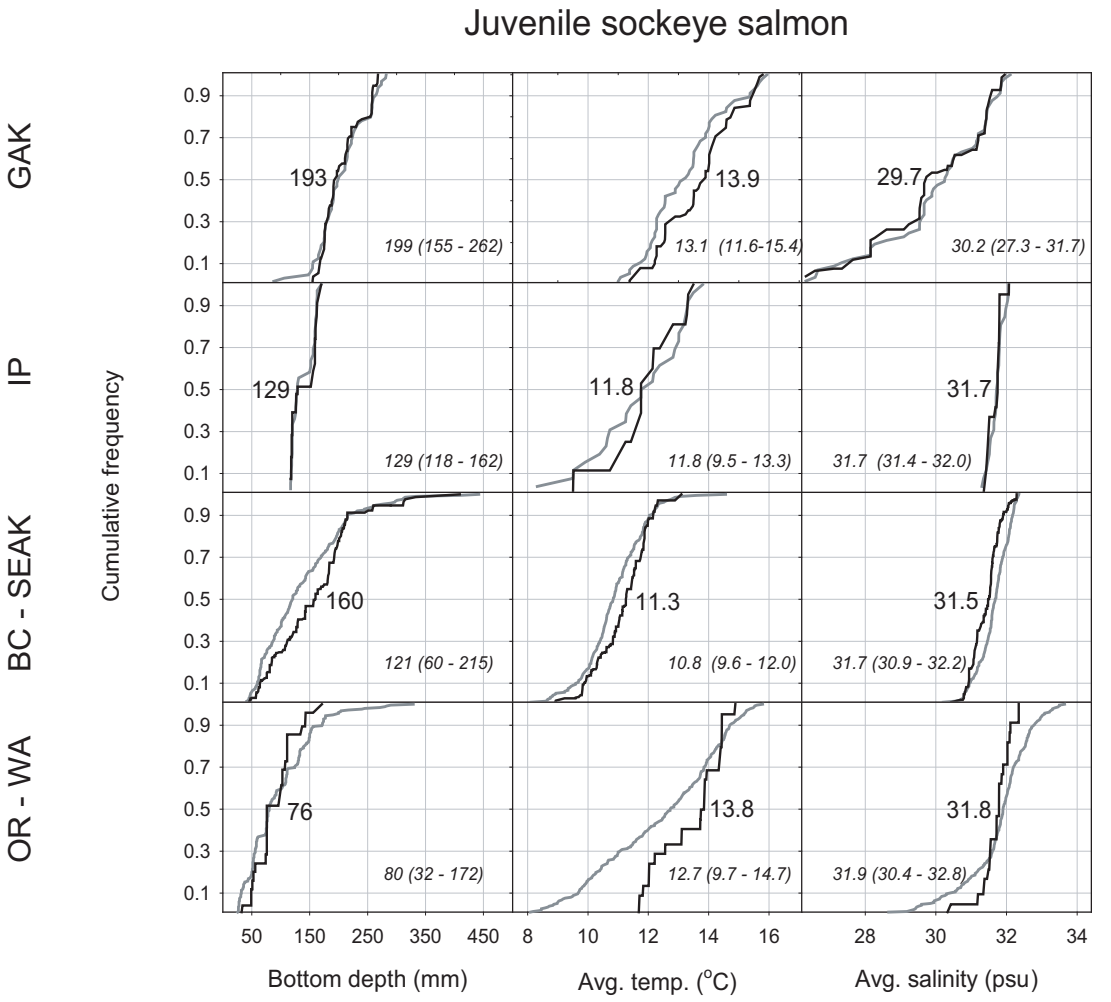


Figure 7. Cumulative frequency distributions of sampling effort (gray lines) and of $\log_{10}$(CPUE+1) of juvenile sockeye salmon (black lines) ordered by bottom depth (left), and temperature (center) and salinity (right) of the upper water column (2–15 m) by region (Figure 1) for all months pooled. Shown in small italics are the medians and ranges (10th–90th percentile) of the three environmental variables during sampling. Shown in larger script are the medians of the three environmental variables relative to the cumulative CPUE of salmon.

Distribution and Abundance of Juvenile Fish Versus Spawning Populations

In general, the latitudinal ranges of the different Pacific salmon along the continental shelf during their first summer and fall in the ocean (Figure 2) were similar to the latitudinal ranges of their parent spawning populations. The rank in relative abundance of adults of the different species of Pacific salmon reported in the literature (pink salmon > chum salmon > sockeye salmon > coho salmon > Chinook salmon; Burgner 1991; Healey 1991; Heard 1991; Sandercock 1991; Salo 1991; Azumaya and Ishida 2004) was similar to the observed rank in relative CPUE of the juvenile fish along the coastal shelf (Figure 2).

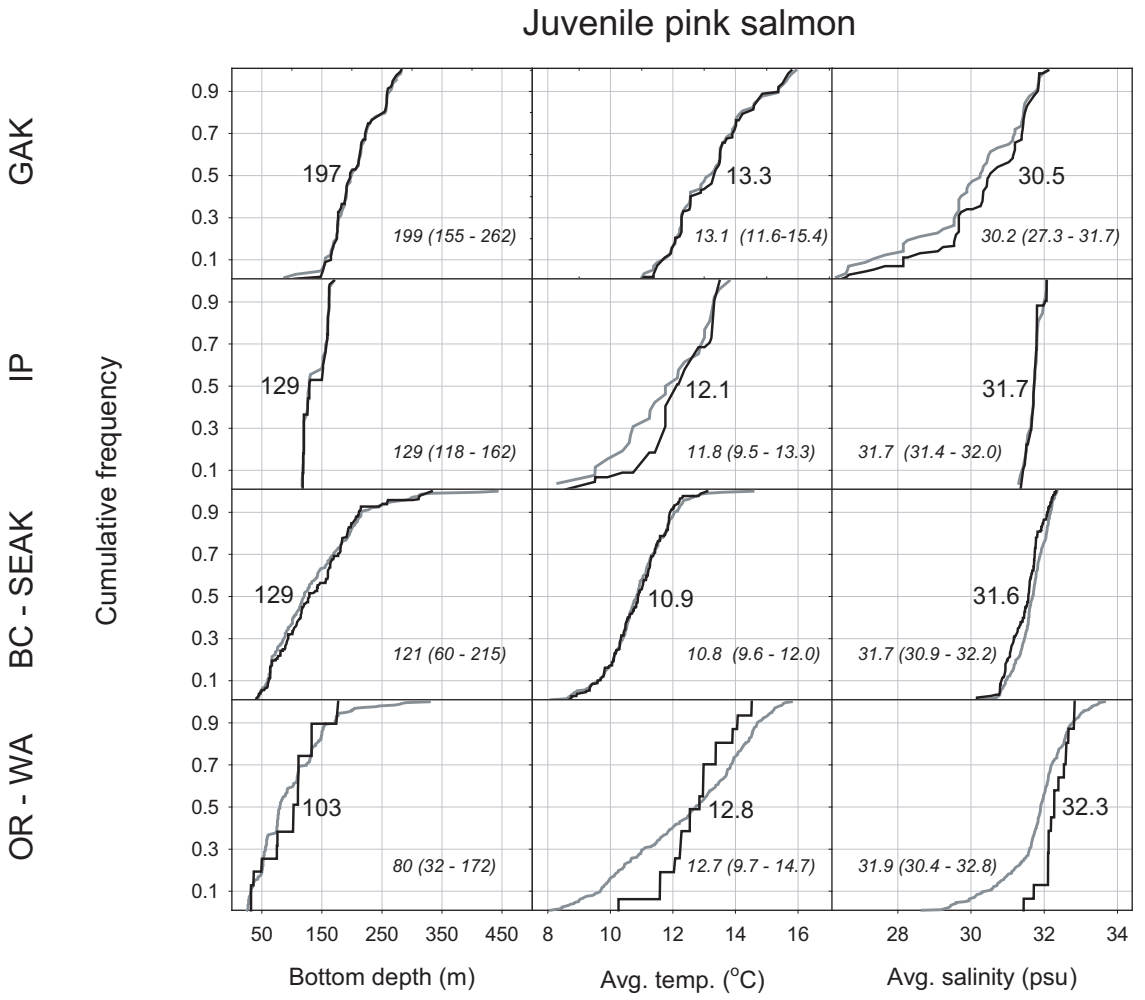


Figure 8. Cumulative frequency distributions of sampling effort (gray lines) and of $\log_{10}$(CPUE+1) of juvenile pink salmon (black lines) ordered by bottom depth (left), and temperature (center) and salinity (right) of the upper water column (2–15 m) by region (Figure 1) for all months pooled. Shown in small italics are the medians and ranges (10th–90th percentile) of the three environmental variables during sampling. Shown in larger script are the medians of the three environmental variables relative to the cumulative CPUE of salmon.

Pink, chum, and sockeye salmon.—Like the coastal abundances of juvenile pink, chum, and sockeye salmon (Figure 2), the North American spawning populations of these species are also greatest from British Columbia north into Alaska. Spawning populations of pink salmon extend from Puget Sound, the Strait of Georgia, the Fraser River, and north to western Alaska and, based on the locations of commercial catches of adult fish, are in greatest abundance in central and southeast Alaska, but are also very large in British Columbia (Heard 1991).

Historically, chum salmon spawned over a very wide geographic range, from Alaska to as far south as Monterey Bay, California (Salo 1991). However, at present, chum salmon spawn only as far south as the north-

Table 7. Median bottom depths, and temperatures and salinities of the upper water column (2–15 m) of the cumulative $\log_{10}$(CPUE+1) distributions of the different juvenile salmon by area for all sampling periods combined (See also Figures 3–8). Regions where the different salmon were fairly abundant (Figure 2) are shaded. Data are restricted to the continental shelf (≤500m depth).

Region	Subyearling Chinook	Yearling Chinook	Juvenile coho	Juvenile chum	Juvenile sockeye	Juvenile pink
Median bottom depth (m)						
GAK	–	258	198	192	193	197
IP	–	160	126	130	129	129
BC-SEAK60	89	93	115	160	129	
OR-WA	53	56	77	111	76	103
CA-OR	46	66	80	78	–	–
C-CA	47	26	–	–	–	–
Median temperature (°C)						
GAK	–	12.3	12.8	13.5	13.9	13.3
IP	–	10.2	12.2	11.8	11.8	12.1
BC-SEAK10.7	11.1	10.9	10.9	11.3	10.9	
OR-WA	11.9	11.7	12.6	13.2	13.8	12.8
CA-OR	10.4	10.8	10.7	11.7	–	–
C-CA	12.5	11.5	–	–	–	–
Median salinity (psu)						
GAK	–	29.7	30.3	30.3	29.7	30.5
IP	–	31.7	31.7	31.7	31.7	31.7
BC-SEAK31.6	31.6	31.7	31.6	31.5	31.6	
OR-WA	32.0	32.0	31.9	31.9	31.8	32.3
CA-OR	33.5	33.1	32.7	31.9	–	–
C-CA	33.5	33.3	–	–	–	–

ern Oregon coast, where populations are small (Johnson et al. 1997). The largest North American populations of chum salmon are in Alaska, British Columbia, and the Puget Sound–Strait of Georgia regions, where annual releases of artificially propagated juvenile chum salmon are also high, averaging during the 1990s about 450 million, 200 million, and 85 million fish, respectively (Johnson et al. 1997; Brodeur et al. 2003).

Sockeye salmon spawning populations are associated with lakes, and Bristol Bay, Alaska (in the Bering Sea) accounts for more than 50% of the total spawning of this species in North America (Burgner 1991). It is unlikely that Bristol Bay juvenile sockeye salmon were caught during this study, since they do not appear to migrate onto the coastal shelf of the Gulf of Alaska (Hartt and Dell 1986). The next largest sockeye salmon spawning populations are associated with lakes of the Fraser River basin, British Columbia. A few of the other major spawning populations are found on Kodiak Island, in central Alaska (the Copper River), in southeast Alaska, in lakes of the Skeena and Nass River basins of northern British Columbia, and the Somass River–Alberni Inlet of western Vancouver Island (Burgner 1991; Beacham et al. 2000). Historically, large populations of sockeye salmon also were found in the Columbia River and Owikeno Lake (central British Columbia), but these are now very much reduced (Burgner 1991; McKinnell et al. 2001).

Coho and Chinook salmon.—Juvenile coho and yearling (stream-type) Chinook salmon were widespread along the coastal shelf (Figure 2), and the spawning populations of both are similarly widespread. Conversely, juvenile subyearling Chinook salmon were only abundant from the west coast of Vancouver Island south to central California (Figure 2), a latitudinal distribution that also matches that of the spawning populations of these ocean-type fish.

Coho salmon spawn throughout the study area, from northern California north through central Alaska, but are most abundant in the center of their range and rarer in the northern and southern parts of their range (Sandercock 1991). Chinook salmon also spawn over a wide latitudinal range from Alaska to central California (Healey 1983; Healey 1991; Myers et al. 1998; USFWS 2001; MacFarlane and Norton 2002). However, most Chinook salmon from Alaskan rivers are stream-type fish, that migrate to the ocean as yearlings (age 1.0) after overwintering in freshwater, whereas many Chinook salmon from northern British Columbia to the Central Valley of California are ocean-type fish, that migrate to the ocean as subyearlings (age 0.0) a few weeks or months after emerging from the gravel (Healey 1983, 1991; USFWS 2001; MacFarlane and Norton 2002; Waples et al. 2004). Although ocean-type spawners are predominant in most rivers in the area from northern British Columbia south into California, stream-type spawners are abundant in the upper basins of some large rivers, such as the Skeena, Fraser, Columbia, Snake, and Willamette rivers (Healey 1983, 1991; Waples et al. 2004). Unlike spawning populations of coho salmon, which are found in low abundance in the southern part of their range in northern California, spawning populations of ocean-type (subyearling) Chinook salmon are found in high abundance in the southern parts of their range in the Klamath basin and Central Valley of California (USFWS 2001; MacFarlane and Norton 2002).

Coho and Chinook salmon are by far the predominant spawners in the streams and major rivers that empty into the ocean along the open Washington, Oregon, and California coast. In this region, hatchery production accounts for a substantial proportion of the total juvenile production of salmon, and almost all of the hatchery production is of these two species (Table 8). In the 3 years of this study, no hatchery pink salmon and only small numbers of hatchery sockeye and chum salmon were released along the open coast south of the WCVI (Table 8).

Distribution of Juvenile Fish Versus Ocean Entry Points

Many of the largest observed abundances of juvenile salmon along the continental shelf were near major river mouths or exit corridors for fish leaving freshwater or protected marine waters and entering the coastal ocean. Major entry points onto the continental shelf varied, of course, among the different species and populations of salmon.

Pink and chum salmon.—Two major production areas for chum and pink salmon are in southeast Alaska and Prince William Sound (Heard 1991; Carlson et al. 2000; Cooney et al. 2001; Boldt and Haldorson 2004). The major exit corridors for pink and chum salmon leaving these areas are thought to be Icy Strait, just to the southeast of our IP sampling area, and the southwest end of Prince William Sound (PWS), just to the northeast of our GAK sampling area (Carlson et al. 2000). During sampling in July and August, between southern southeast Alaska and the Alaska Peninsula west of Kodiak Island, Carlson et al. (2000) found that the highest CPUE of pink and chum salmon occurred in areas north and west of southeast Alaska along the central Alaskan shelf to the west

Table 8. Total releases (in millions) of juvenile hatchery salmon in 2000, 2002, and 2004 between the west coast of Vancouver Island and central California adjacent to our coastal sampling regions (Figure 1). Besides releases in smaller coastal rivers, the OR-WA, N-CA (northern California), and C-CA regions include releases in the Columbia River basin, the Klamath/Trinity River basins, and the Sacramento/San Joaquin River basins of the Central Valley, respectively. Because subyearling (age-0.0) Chinook salmon were released during much of the year, their range in average size at release was great. Those subyearling Chinook salmon greater than 120 mm FL or more than 18 g were called large.

					Chinook salmon	
Release area	Pink salmon	Sockeye salmon	Chum salmon	Coho salmon yearlings	small: subyearlings	large: yearlings and subyearlings
WCVI	0	0.9	98.9	3.9	46.0	<0.1
OR-WA	0	4.0	5.4	96.8	227.8	88.7
CA-OR	0	0	0	1.4	2.2	10.4
N-CA	0	0	0	0[b]	24.5	6.9
C-CA	0	0	0	0	51.5	2.7

Source: the Pacific States Marine Fisheries Commission Regional Mark Processing Center: http://www.rmpc.org/, last accessed 2/10/2006.

[a] Does not include 12.6 million fry and fingerling (age 0.0) fish released in the WCVI and OR-WA regions.

[b] Small numbers (approximately 0.6 million in 2000) of age-1.0 coho salmon were released in the Klamath/Trinity system (USFWS 2001). These were not in the Regional Mark Processing Center database.

of PWS. Where our sampling overlapped with that of Carlson et al. (2000), we found a similar abundance pattern for chum and pink salmon: higher abundances at IP and GAK, near the major exit corridors from southeast Alaska and PWS, and lower abundances off SEAK (Figure 2).

High abundances of both juvenile pink and chum salmon also occurred in C-BC (Figure 2). All of the sampling in this study was from even years, when juvenile pink salmon from the Fraser River are dominant (Heard 1991; Beamish et al. 2003). In these years, large numbers of pink salmon from the Fraser River probably migrated north through Johnstone and Queen Charlotte Straits, contributing to the high abundance of pink salmon we observed in the C-BC region (Figure 2). The Fraser River is also a major producer of chum salmon (Beamish and Folkes 1998; Ryall 1998), and many would be expected to migrate north into the C-BC area.

Catch per unit effort of chum salmon in June and July off the WCVI was also high (Figure 2). But large numbers of hatchery chum salmon are released from the WCVI between March and May (Table 8), undoubtedly contributing to the large CPUE of this species in June and July in this area.

Sockeye salmon.—The major exit corridor for sockeye salmon emigrating from the Fraser River, the largest source of sockeye salmon in our sampling area, is thought to be Queen Charlotte Strait (Groot and Cooke 1987; Burgner 1991; Beamish et al. 2003), which opens onto Queen Charlotte Sound in the C-BC sampling area (Figure 1). Most Fraser River yearling smolts are believed to leave the Strait of Georgia by late June and July (Groot and Cooke 1987; Burgner 1991), which is the same time period when we caught large numbers in C-BC. Sockeye salmon from the Skeena and Nass Rivers also enter the C-BC area, but at the northern end of Hecate Strait (or eastern end of Dixon En-

trance). These populations of juvenile sockeye salmon undoubtedly were responsible for the very high abundance we observed in June and July in the C-BC area (Figure 2). On the other hand, genetic stock identification indicates that local fish from the Somass River–Alberni Inlet system together with a smaller fraction of fish from the Fraser River account for more than 80% of the sockeye salmon caught off WCVI in June and July (M. Trudel, unpublished data).

Coho salmon.—In June and July, the largest abundances of coho salmon were in the OR-WA and WCVI regions (Figure 2). Large numbers of juvenile coho salmon are released from hatcheries to the Columbia River and coastal Washington rivers (Table 8) and enter the WA-OR region in spring. Genetic stock identification indicated that most of our samples of coho salmon in this region originated from the Columbia River and Washington and Oregon coasts regardless of the sampling season (Teel et al. 2003; Van Doornik et al. in press). Conversely, relatively few coho salmon were released from hatcheries in WCVI (Table 8). Many of the coho salmon found in WCVI in June had migrated there from Puget Sound, the Strait of Georgia, the Columbia River, and the Washington coast. This was confirmed by both genetic stock identification and from recoveries of coded-wire tagged fish (Trudel et al. 2004; Morris et al. 2007,this volume). Interestingly, the relatively low abundance of coho salmon during both seasons in the C-BC region (compared to coho salmon abundances in other regions) suggests that this region may not be as important a collecting area or migration route for juvenile coho salmon as it is for the juvenile sockeye, pink, and chum salmon from British Columbia. The relatively high abundance and F.O. of juvenile coho salmon at IP in both seasons may be partly a consequence of its proximity to the Icy Strait exit corridor (Figure 2).

Yearling Chinook salmon.—As was the case for coho salmon, the highest CPUEs of yearling Chinook salmon during the early season occurred in OR-WA and WCVI (Figure 2). Many yearling smolts were released from hatcheries in the OR-WA area, mainly in the Columbia River basin (Table 8). Releases of yearling Chinook from WCVI were low. Genetic stock identification indicated (for a different set of years) that more than 50% of the yearling Chinook salmon caught in June in southern British Columbia originated in the Columbia River (Trudel et al. 2004).

Subyearling Chinook salmon.—In June and July, the abundance of subyearling Chinook salmon was high only in two regions, C-CA and OR-WA (Figure 2), which are adjacent to two very large sources of hatchery subyearling fish: the Central Valley of central California and the Columbia River, respectively (Table 8). Chinook salmon smolts from the Central Valley enter the San Francisco estuary between April and June, and most leave the estuary and enter the ocean by the end of June (Kjelson et al. 1982; MacFarlane and Norton 2002). Thus, they were vulnerable to capture in June and July on the coastal shelf in C-CA (Figure 2). In the Columbia River, however, downstream migration of subyearling Chinook salmon is protracted, lasting mainly from March into October, but peaking in June or early July (Dawley et al. 1985). The catch of subyearling fish in June in OR-WA (Figure 2) represents in the early part of this seaward migration from the Columbia River.

In general, the seaward migration of subyearling smolts in rivers from British Columbia to northern California is protracted, sometimes lasting much of the summer and including a period of estuarine residence (Reimers 1973; Myers and Horton 1982; Dawley et al. 1985; Fisher and Pearcy 1990; Healey 1991; USFWS 2001). Our sampling in June in WCVI and CA-OR, was probably too ear-

ly to catch many subyearling fish. More subyearlings were caught in the later season in both regions (Figure 2). Genetic stock identification indicated that in the CA-OR region in August 2000, most Chinook salmon (subyearlings and yearlings pooled) originated in the area from the Central Valley to southern Oregon (Brodeur et al. 2004).

Seasonal Shifts in Distribution Versus Migration

Hartt and Dell (1986) examined CPUE data for juvenile salmon caught with purse seines between April and October 1956–1970 over a wide extent of the Gulf of Alaska, Aleutian Island region, and Bering Sea. They identified a counterclockwise shift (to the northwest, west, and southwest) between spring and fall in the abundances of juvenile sockeye, pink, chum, and coho salmon along the continental shelf of the Gulf of Alaska. They found that the CPUE of salmon in seines held open to the south was, on average, about five times greater than the CPUE of salmon in seines held open to the north, suggesting active northward migration of juvenile fish. Finally, they observed that most juvenile salmon tagged in coastal regions of the Gulf of Alaska and Alaska Peninsula were later caught as adults in a clockwise direction from where they were released (i.e., to the northeast, east, or southeast, depending on where they were released). From these three major lines of evidence, they developed a model of counterclockwise migration of juvenile salmon along the continental shelf of the Gulf of Alaska.

Additional evidence for northward or counterclockwise migration of juvenile salmon off Oregon and Washington and in the Gulf of Alaska has come from recoveries at sea of juvenile coded-wired tagged (CWT) and thermally marked fish released from hatcheries. Pearcy and Fisher (1988) and Fisher and Pearcy (1995) found that by late summer off Oregon and Washington most CWT coho and Chinook salmon had migrated north of where they were released. Orsi and Jaenicke (1996) and Orsi et al. (2000) found yearling (age 1.0) Chinook and coho salmon in southeastern Alaska that had migrated north from the Columbia River. Morris et al. (2007) demonstrated counterclockwise coastal migration for CWT coho salmon released from each of six different regions between the Oregon coast and southeastern Alaska. Finally, Carlson et al. (2000) very clearly demonstrated counterclockwise migration of thermally marked hatchery pink and chum salmon from their release locations in southeast Alaska and Prince William Sound.

Genetic stock identification also lends support to the counterclockwise migration model for juveniles of certain stocks of salmon. For example, Trudel et al. (2004) found that about one-half of the juvenile Chinook salmon caught during the summer off British Columbia and southeastern Alaska originated in the Columbia River, and of these Columbia River fish, most were spring-run (and stream-type) fish from the upper basin and Snake River.

The regional shifts in abundance of juvenile salmon between seasons or between months that we observed in this study were, in general, consistent with the counterclockwise migration model of Hartt and Dell (1986). For example, CPUE and F.O. of coho, chum, sockeye, and pink salmon either peaked later and/or remained high for a longer period of time at GAK in the northwestern Gulf of Alaska than at IP in the northeastern Gulf of Alaska (Table 5), a result consistent with westerly migration of these fish across the northern Gulf of Alaska during their first summer in the ocean. In addition, there is no evidence from the regional shifts in abundance for eastward or southward migration between the seasons (Figure 2).

However, our abundance data do suggest that the pace and extent of the counterclock-

wise migration may vary greatly among different species and life history types of salmon. The most dramatic shift in abundance to the north and west between seasons was that of sockeye salmon, many of which were probably from the Fraser River (Figure 2). During their first summer in the ocean, sockeye salmon apparently migrate quickly in a counterclockwise direction around the Gulf of Alaska. The abundance of chum salmon also shifted to the north between the early and late seasons, decreasing at WCVI and to the south and also at IP, but increasing at SEAK and at GAK while remaining about the same at C-BC (Figure 2; Table 5).

Yearling Chinook salmon may also migrate rapidly to the north and also offshore. Between seasons, the CPUE and F.O. of yearling Chinook salmon decreased greatly in OR-WA and WCVI, the two areas where they were most abundant in early summer, which is consistent with migration of this life history type out of these two regions. However, no concomitant increase in abundance of these fish occurred in regions to the north, thus providing little direct evidence for northward migration (Figure 2). Nevertheless, tag recoveries (Hartt and Dell 1986; Orsi and Jaenicke 1996; Orsi et al. 2000) indicate rapid northward migration of some yearling Chinook salmon during the summer. In fact, most tagged yearling Chinook salmon caught between June and September in outside waters of southeast Alaska originated in Washington or Oregon (Orsi and Jaenicke 1996; Orsi et al. 2000). The very low abundance of yearling Chinook salmon during the late season in all regions (Figure 2) would be consistent with relatively early off shelf movement of fish of southern origin into deeper waters of the Gulf of Alaska, a suggestion also made by Hartt and Dell (1986), or with movement to depths below our sampling gear. Unlike the fish originating in Oregon and Washington, many of the yearling Chinook salmon originating in southeast Alaska and British Columbia remain through the fall and winter in inside waters (Orsi and Jaenicke 1996; Orsi et al. 2000) or in inside waters and on the open shelf (Morris et al. 2004; Trudel et al. 2004).

In contrast to the hypothesized rapid migrations of sockeye and yearling Chinook salmon, migrations of some chum and pink salmon from British Columbia may be quite slow. Between seasons there was little change in abundance of pink or chum salmon in C-BC (Figure 2). Similarly, in the 1990s, large numbers of juvenile pink and chum salmon also were found in the inside waters of the Strait of Georgia well into the fall (Beamish and Folkes 1998; Beamish et al. 2003). These data suggest that the alongshore coastal migrations of some British Columbia pink and chum salmon stocks may be quite slow, with many fish feeding in the Strait of Georgia, Queen Charlotte Sound, Hecate Strait, and Dixon Entrance areas for several months during the summer and early to late fall. Recent survey data indicate that by February, in most years, pink and chum salmon have moved off the shelf and into deeper water or north of southeast Alaska (Morris et al. 2004).

The northward shift in abundance of coho salmon between the early and late sampling seasons was quite subtle, CPUE and F.O. decreasing only moderately in regions from SEAK south and increasing only moderately at IP and GAK (Figure 2). This result suggests that the northward migration of coho salmon may be relatively slow and prolonged, and some individuals may not migrate far. For example, coho salmon were still being caught in September at IP, after chum, sockeye, and pink salmon had already left the area (Table 5). Similarly, at GAK, the peak in abundance and F.O. of coho salmon was not reached until October, long after the peak in abundance of chum, sockeye, and pink salmon (Table 5).

Pearcy and Fisher (1988) also found that CPUE of juvenile coho salmon in the Oregon–Washington area decreased only moderately between June and September and that coded-wire-tagged fish from the Columbia River and coastal Oregon locations were still present off Washington in September, suggesting that a fairly substantial portion of this southern population of coho salmon remained over the entire summer near where they entered the ocean. Recent genetic stock identification of coho salmon confirms that Columbia River, coastal Oregon, and coastal Washington fish comprise most of the catch in both June and September in the OR-WA region, with some influx of Puget Sound coho onto the Washington shelf in September (Teel et al. 2003; Van Doornik et al. in press). However, data from recoveries of fish tagged as juveniles and subsequently recovered as adults (Hartt and Dell 1986) also clearly indicate that some juvenile coho salmon migrate rapidly to the north and west in the Gulf of Alaska during their first summer. In addition, Morris et al. (2007) determined from recoveries of CWT fish that both fast- and slow-migrating coho salmon often originate in the same river basins.

Finally, the absence in both the early and late seasons of subyearling (ocean-type) Chinook salmon in areas north of where their parent spawning populations occur, coupled with their fairly high abundances in southern regions in the late season, suggests that their migrations during the summer and early fall may be quite limited in extent (Figure 2).

Although the temporal shifts in abundance of juvenile salmon are largely consistent with the counterclockwise migration model of juvenile salmon in the Gulf of Alaska, it is important to keep in mind that temporal changes in the abundance of juvenile salmon in regions of the continental shelf are also determined by processes other than alongshore migration, including (1) the migration of fish from local inside waters onto the open shelf (e.g., Orsi et al. 2000; Cooney et al. 2001; Jaenicke and Celewycz 1994), (2) the migration of fish off the shelf into deeper water or to depths below our sampling gear, and (3) mortality. Furthermore, interannual variability in abundance and the timing and rates of migration of the different species and life history types of salmon may be high. For example, between the early and late seasons in 2004, the CPUE of sockeye salmon decreased greatly in BC-SEAK while increasing moderately at GAK, a result consistent with northward (or offshore) migration of sockeye salmon out of the BC-SEAK area and of immigration of sockeye salmon to the GAK area (Appendix A, Figure A15). However, between seasons in 2000, little change occurred in the CPUE of sockeye salmon in BC-SEAK north of Vancouver Island, providing little evidence for emigration of fish from the BC-SEAK area (Appendix A, Figure A13). Repeated monitoring over a period of years at different locations along the coast will be needed in order to understand how the migrations of the different juvenile salmon may respond to changing oceanographic conditions on interannual or interdecadal time scales.

Salmon Distribution Versus Depth, Temperature, and Salinity

The results of this and previous studies indicate a strong association between Chinook salmon, particularly subyearling Chinook salmon, and the shallow inshore regions of the coastal shelf. In all regions where they occurred, subyearling Chinook salmon were distributed in shallower water than the other juvenile salmonids (Figure 4; Table 7). In the regions where they were most abundant (from BC-SEAK south), yearling Chinook salmon also were found in shallower water than the other four species of salmon (Figure 3; Table 7). A shallow distribution of Chinook salmon was also apparent from an ordination analysis

by Orsi et al. (2007, this volume) of the fish and squid assemblages caught in the coastal zone, in which juvenile Chinook salmon had the shallowest position of all salmon species along the axis most strongly correlated with bottom depth. Similar nearshore distributions for subyearling Chinook salmon have been reported in the area bracketing the mouth of the Columbia River (Miller et al. 1983) and in the CA-OR and OR-WA regions (Fisher and Pearcy 1995; Brodeur et al. 2004, 2005). Miller et al. (1983) found that the abundance of Chinook salmon less than 130 mm FL was much greater in very shallow water (<9 m bottom depth) than in deeper water (>30 m bottom depth). From this result, they concluded that offshore movement of Chinook salmon was size-dependent.

Evidence of depth preferences among the other species is less clear. Coho salmon were very rare over water deeper than about 250 m, and in CA-OR and BC-SEAK, where a significant fraction of the sampling was over deeper water, they were most abundant between about 30-m and 150–175-m bottom depth (Figure 5). However, in IP and GAK, coho salmon were caught routinely out to 250-m bottom depth (Figure 5). Although in OR-WA and BC-SEAK, chum, sockeye, and pink salmon tended to occur in deeper water than Chinook or coho salmon (Table 7), in the regions where they were most abundant, the depth distributions of the three "northern" salmon species usually followed the depth distributions of the sampling over the continental shelf fairly closely (Figures 6–8).

Within regions, evidence of temperature or salinity preferences was lacking generally among the different salmon species, especially in regions where the fish were abundant (Figures 3–8). There were some exceptions. For example, consider OR-WA where coho salmon were not found in the coldest or most saline water associated with inshore coastal upwelling (Figure 5) and where abundance of subyearling Chinook salmon in the nearshore, cold, and saline waters was high (Figure 4). The distribution of Chinook salmon likely indicates a preference to stay close to shore in shallow water, rather than a preference for a particular salinity regime. Exceptions also occurred in regions where juvenile salmon occurred infrequently. For example, in OR-WA, chum, sockeye, and pink salmon were largely absent from the warmest and freshest water associated with river plumes and were not found in the coldest and most saline water associated with coastal upwelling (Figures 6–8).

Across regions, however, there was an obvious association between salinity and species. Subyearling Chinook salmon were most abundant in the areas of high salinity found to the south, yearling Chinook and coho salmon were abundant across a wide range of salinity, and chum, sockeye, and pink salmon were most abundant in areas of low salinity found to the north (Table 7).

Conclusion

Combining information on the coastal distribution and abundance of juvenile salmon, and how it changes seasonally, with stock-specific information on catch composition and migration provided by CWTs, thermal marks , and genetic stock identification (e.g., Carlson et al. 2000; Teel et al. 2003; Brodeur et al. 2004; Trudel et al. 2004; Morris et al. 2007; Van Doornik et al., in press), should produce a more detailed understanding of the early ocean life of the different salmon stocks along the west coast of North America. Knowledge of the timing and migration routes of specific stocks of salmon will allow us to know when and where to look for biotic and abiotic environmental factors that may be critical in determining growth rates (e.g., Trudel et al. 2007b, this volume) and variability in survival at interannual and interdecadal frequencies (Mantua et al. 1997; Peterson and

Schwing 2003). Combining data on the food utilization (e.g., Brodeur et al. 2007; this volume), the community of potential predators and competitors (e.g., Orsi et al. 2007), and physical environment (e.g., this paper) with which the juvenile salmon are associated will also provide more complete insights into the different environments the juvenile salmon encounter along their migrations.

Acknowledgments

Funding for the various studies was provided by the Bonneville Power Administration, the Canadian Department of Fisheries and Oceans, the Juneau Center for Fisheries and Ocean Sciences, the National Science Foundation, and the Northwest, Southwest, and Alaska NMFS Science Centers. Bill Pearcy, Bill Peterson, David Teel, Laurie Weitkamp, and an anonymous reviewer provided very constructive and helpful comments on an earlier version of this manuscript. This is contribution number 328 to the U.S. GLOBEC program.

References

Azumaya, T., and Y. Ishida. 2004. An evaluation of the potential influence of SST and currents on the oceanic migration of juvenile and immature chum salmon (*Oncorhynchus keta*) by a simulation model. Fisheries Oceanography 13:10–23.

Batchelder, H. P., J. A. Barth, P. M. Kosro, P. T. Strub, R. D. Brodeur, W. T. Peterson, C. T. Tynan, M. D. Ohman, L. W. Botsford, T. M. Powell, F. B. Schwing, D. G. Ainley, D. L. Mackas, B. M. Hickey, and S. R. Ramp. 2002. The GLOBEC Northeast Pacific California Current System Program. Oceanography 15:36–47.

Beacham, T. D., C. C. Wood, R. E. Withler, K. D. Le and K. M. Miller. 2000. Application of microsatellite DNA variation to estimation of stock composition and escapement of Skeena River sockeye salmon (*Oncorhychus nerka*). North Pacific Anadromous Fish Commission Bulletin 2:263–276.

Beamish, R. J., and M. Folkes. 1998. Recent changes in the marine distribution of juvenile chum salmon off Canada. North Pacific Anadromous Fish Commission Bulletin 1:443–453.

Beamish, R. J., I. A. Pearsall, and M. C. Healey. 2003. A history of the research on the early marine life of Pacific salmon off Canada's Pacific coast. North Pacific Anadromous Fish Commission Bulletin 3:1–40.

Boldt, J. L., and L. J. Haldorson. 2004. Size and condition of wild and hatchery pink salmon juveniles in Prince William Sound, Alaska. Transactions of the American Fisheries Society 133:173–184.

Brett, J. R. 1979. Environmental factors and growth. Pages 599–675 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume VIII, bioenergetics and growth. Academic Press, New York, San Francisco, London.

Brodeur, R. D., K. W. Myers, and J. H. Helle. 2003. Research conducted by the United States on the early ocean life history of Pacific salmon. North Pacific Anadromous Fish Commission Bulletin 3:89–131.

Brodeur, R. D., J. P. Fisher, D. J. Teel, R. L. Emmett, E. Casillas, and T. W. Miller. 2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the northern California Current. Fishery Bulletin 102:25–46.

Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Marine Ecology Progress Series 298:41–57.

Brodeur, R. D., E. A. Daly, M. V. Sturdevant, T. W. Miller, J. H. Moss, M. Thiess, M. Trudel, L. A. Weitkamp, J. Armstrong, and E. C. Norton. 2007. Regional comparisons of juvenile salmon (Oncorhynchus spp.) feeding in coastal marine waters off the west coast of North America. Pages xxx–xxx *in* G. Churchill, R. Brodeur, L. Haldorson, and S. McKinnell, editors. Ocean ecology of salmon in western North America: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Burgner, R. L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). Pages 1–117 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC Press, University of British Columbia, Vancouver.

Carlson, H. R., E. V. Farley, Jr., and K. W. Myers. 2000. The use of thermal otolith marks to determine stock-specific ocean distribution and migration patterns of Alaskan pink and chum salmon in the North Pacific Ocean 1996–1999. North Pacific Anadromous Fish Commission Bulletin 2:291–300.

Cooney, R. T., J. R. Allen, M. A. Bishop, D. L. Eslinger, T. Kline, B. L Norcross, C. P. McRoy, J. Milton, J. Olsen, V. Patrick, A. J. Paul, D. Salmon, D. Scheel, G. L. Thomas, S. L. Vaughan, and T. M. Willette. 2001. Ecosystem control of pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring (*Clupea pallasii*) populations in Prince William Sound, Alaska. Fisheries Oceanography 10(Supplement 1):1–13.

Davis, N. D., K. W. Myers, and Y. Ishida. 1998. Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. North Pacific Anadromous Fish Commission Bulletin 1:146–162.

Dawley, E. M., R. D. Ledgerwood, and A. Jensen. 1985. Beach and purse seine sampling of juvenile salmonids in the Columbia River estuary and ocean plume, 1977–1983; volume I procedures, sampling effort, and catch data. NOAA Technical Memorandum NMFS F/NWC-74.

Emmett, R. L., R. D. Brodeur, and P. M. Orton. 2004. The vertical distribution of juvenile salmon (*Oncorhynchus* spp.) and associated fishes in the Columbia River Plume. Fisheries Oceanography 13:392–402.

Fisher, J. P., and W. G. Pearcy. 1988. Growth of juvenile coho salmon (*Oncorhynchus kisutch*) in the ocean off Oregon and Washington, USA, in years of differing coastal upwelling. Canadian Journal of Fisheries and Aquatic Sciences 45:1036–1044.

Fisher, J. P., and W. G. Pearcy. 1990. Distribution and residence times of juvenile fall and spring chinook salmon in Coos Bay, Oregon. Fishery Bulletin 88:51–58.

Fisher, J. P., and W. G. Pearcy. 1995. Distribution, migration, and growth of juvenile chinook salmon, *Oncorhynchus tshawytscha,* off Oregon and Washington. Fishery Bulletin 93:274–289.

Groot, C., and K. Cooke. 1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? Pages 53–60 *in* H. D. Smith, L. Margolis, and C.C. Wood, editors. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management: proceedings of the international sockeye symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 96.

Hartt, A. C., and M. B. Dell. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. International North Pacific Fisheries Commission Bulletin 46.

Healey, M. C. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type Chinook salmon, *Oncorhynchus tshawytscha*. Canadian Field-Naturalist 97:427–433.

Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311– 393 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC Press, University of British Columbia, Vancouver.

Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). Pages 119–230 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC Press, University of British Columbia, Vancouver.

Huyer, A. 1983. Coastal upwelling in the California Current system. Progress in Oceanography 12:259–284.

Jaenicke, H. W., and A. G. Celewycz. 1994. Marine distribution and size of juvenile Pacific salmon in Southeast Alaska and northern British Columbia. Fishery Bulletin 92:79–90.

Johnson, O. W., W. S. Grant, R. G. Kope, K. Neely, F. W. Waknitz, and R. S.Waples. 1997. Status review of chum salmon from Washington, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-32.

Kjelson, M. A., P. F. Raquel, and F. W. Fisher. 1982. Life history of fall-run juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento–San Joaquin Estuary, Cali-

fornia. Pages 393–411 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Koo, T. S. Y. 1962. Age designation in salmon. Pages 41–48 *in* T. S. Y. Koo, editor. Studies of Alaska red salmon. University of Washington Press, Seattle.

Krutzikowsky, G. K., and R. L. Emmett. 2005. Diel differences in surface trawl catches off Oregon and Washington. Fisheries Research 71:365–371.

Logerwell, E. A., N. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12:554–568.

MacFarlane, R. B., and E. C. Norton. 2002. Physiological ecology of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco estuary and Gulf of the Farallones, California. Fishery Bulletin 100:244–257.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McKinnell, S. M., C. C. Wood, D. T. Rutherford, K. D. Hyatt, and D. W. Welch. 2001. The demise of Owikeno Lake sockeye salmon. North American Journal of Fisheries Management 21:774–791.

Miller, D. R., J. G. Williams, and C. W. Sims. 1983. Distribution, abundance and growth of juvenile salmonids off the coast of Oregon and Washington, summer 1980. Fisheries Research 2:1–17.

Morris, J. F. T., M. Trudel, M. E. Thiess, R. M. Sweeting, J. Fisher, S. Hinton, J. A. Orsi, E. V. Farley, Jr., and D. W. Welch. 2007. Stock-specific migrations of juvenile coho salmon derived from coded-wire tag recoveries on the continental shelf of western North America. Pages xxx–xxx *in* G. Churchill, R. Brodeur, L. Haldorson, and S. McKinnell, editors. Ocean ecology of salmon in western North America: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Morris, J. F. T., M. Trudel, D. W. Welch, M. E. Thiess, T. B. Zubkowski, and H. R. C. MacLean. 2004. Canadian highseas salmon surveys in the fall of 2003 and the winter of 2004: seasonal changes in the distributions of juvenile salmon on the continental shelf off British Columbia and southeast Alaska. North Pacific Anadromous Fish Commission Document 780.

Myers, J. M., R. G. Kope, G. J. Bryant, D. Teel, L. J. Lierheimer, T. C. Wainwright, W. S. Grant, F. W. Waknitz, K. Neely, S. T. Lindley, and R. S. Waples. 1998. Status review of Chinook salmon from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-35.

Myers, K. W., and H. F. Horton. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. Pages 377–392 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Orsi, J. A., J. A. Harding, S. S. Pool, R. D. Brodeur, L. J. Haldorson, J. M. Murphy, J. H. Moss, E. V. Farley, Jr., R. M. Sweeting, J. F. T. Morris, M. Trudel, R. J. Beamish, and R. L. Emmett. 2007. Epipelagic fish assemblages associated with juvenile Pacific salmon in neritic waters of the California Current and the Alaska Current. Pages xxx–xxx *in* G. Churchill, R. Brodeur, L. Haldorson, and S. McKinnell, editors. Ocean ecology of salmon in western North America: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Orsi, J. A., and H. W. Jaenicke. 1996. Marine distribution and origin of prerecruit chinook salmon, *Oncorhynchus tshawytscha,* in southeastern Alaska. Fisheries Bulletin 94:482–497.

Orsi, J. A., M. V. Sturdevant, J. M. Murphy, D. G. Mortensen, and B. L. Wing. 2000. Seasonal habitat use and early marine ecology of juvenile Pacific salmon in southeastern Alaska. North Pacific Anadromous Fish Commission Bulletin 2:111–122.

Orsi, J. A., and A. C. Wertheimer. 1995. Marine vertical distribution of juvenile Chinook and

coho salmon in southeastern Alaska. Transactions of the American Fisheries Society 124:159–169.

Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. Washington Sea Grant Program, University of Washington Press, Seattle and London.

Pearcy, W. G., and J. P. Fisher. 1988. Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean. Fishery Bulletin 86:173–195.

Peterson, W. T., and F. B. Schwing. 2003. A new climate regime in northeast pacific ecosystems. Geophysical Research Letters 30(17):1896.

Reimers, P. E. 1973. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Research Reports of the Fish Commission of Oregon 4:1–43.

Royer, T. C. 1982. Coastal fresh water discharge in the Northeast Pacific. Journal of Geophysical Research 87:2017–2021.

Ryall, P. 1998. Evaluation of the reliability of in-season run size estimation techniques used for southern British Columbia chum salmon (*Oncorhynchus keta*) runs. North Pacific Anadromous Fish Commission Bulletin 1:380–387.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. 3rd edition. Freeman., New York.

Salo, E. O. 1991. Life history of chum salmon (*Oncorhynchus keta*). Pages 231–309 in C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC Press, University of British Columbia, Vancouver.

Sandercock, F. K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). Pages 395–445 in C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC Press, University of British Columbia, Vancouver.

Teel, D. J., D. M. Van Doornik, and D. R. Kuligowski. 2003. Genetic analysis of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington reveals few Columbia River wild fish. Fishery Bulletin 101:640–652.

Trudel, M., S. R. M. Jones, M. E. Thiess, J. F. T. Morris, D. W. Welch, R. M. Sweeting, J. H. Moss, B. L. Wing, E. V. Farley, Jr., R. E. Baldwin, and K. C. Jacobson. 2007a. Infestations of motile salmon lice on Pacific salmon along the west coast of North America. Pages xxx–xxx *in* G. Churchill, R. Brodeur, L. Haldorson, and S. McKinnell, editors. Ocean ecology of salmon in western North America: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Trudel, M., M. E. Thiess, C. Bucher, E. V. Farley, Jr., B. MacFarlane, E. Casillas, J. F. T. Morris, J. M. Murphy, and D. W. Welch. 2007b. Regional variation in the marine growth and energy accumulation of juvenile Chinook salmon and coho salmon along the west coast of North America. Pages xxx–xxx *in* G. Churchill, R. Brodeur, L. Haldorson, and S. McKinnell, editors. Ocean ecology of salmon in western North America: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Trudel, M., D. W. Welch, J. F. T. Morris, J. R. Candy, and T. D. Beacham. 2004. Using genetic markers to understand the coastal migration of juvenile coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*). North Pacific Anadromous Fish Commission Technical Report 5:52–54.

USFWS (U.S. Fish and Wildlife Service). 2001. Juvenile salmonid monitoring on the mainstem Klamath River at Big Bar and mainstem Trinity River at Willow Creek, 1997–2000. Annual report of the Klamath River Fisheries Assessment Program. Arcata Fish and Wildlife Office, Arcata, California.

U.S. GLOBEC. 1994. Eastern boundary current program, a science plan for the California Current. U.S. GLOBEC Report 11. University of California, Berkeley.

Van Doornik, D. M., D. J. Teel, D. R. Kuligowski, C. A. Morgan, and E. Casillas. In press. Genetic analyses provide insight into the early ocean stock distribution and survival of juvenile coho salmon off the coasts of Washington and Oregon. North American Journal of Fisheries Management 27.

Walker, R. V., K. W. Myers, N. D. Davis, K. Y. Aydin, and K. D. Friedland. 2000. Using temperatures from data storage tags in bioenergetic models of high-seas salmon growth. North Pacific Anadromous Fish Commission Bulletin 2:301–308.

Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshall. 2004. Life-history divergence in Chinook salmon: historic contingency and parallel evolution. Evolution 58:386–403.

Welch, D. W., J. F. T. Morris, M. E. Thiess, M. Trudel, and D. J. Anderson. 2003. CCGS W.E. Ricker Gulf of Alaska salmon survey, June 27 to July 6, 2000. Canadian Data Report of Fisheries and Aquatic Sciences 1125.

Welch, D. W., J. F. T. Morris, M. E. Thiess, M. Trudel, A. R. Ladouceur, T. B. Zubkowski, M. C. Jacobs, P. M. Winchell, and H. R. MacLean. 2004. CCGS W.E. Ricker Gulf of Alaska salmon survey, October 17 to November 9, 2002. Canadian Data Report of Fisheries and Aquatic Sciences 1138.

Weingartner, T. J., K. Coyle, B. Finney, R. Hopcroft, T. Whitledge, R. Brodeur, M. Dagg, E. Farley, D. Haidvogel, L. Haldorson, A. Hermann, S. Hinckley, J. Napp, P. Stabeno, T. Kline, C. Lee, E. Lessard, T. Royer, and S. Strom. 2002. The northeast Pacific GLOBEC Program: coastal Gulf of Alaska. Oceanography 15:48–63.

Wertheimer, A. C., and F. P. Thrower. 2007. Mortality rates of chum salmon during their early marine residency. Pages xxx–xxx *in* G. Churchill, R. Brodeur, L. Haldorson, and S. McKinnell, editors. Ocean ecology of salmon in western North America: regional comparisons. American Fisheries Society, Symposium 57, Bethesda, Maryland.

Appendix A. Distribution maps by month in 2000, 2002, and 2004, of CPUE of subyearling Chinook salmon, yearling Chinook salmon, and juvenile coho salmon, chum salmon, pink salmon, and sockeye salmon in six regions from the central California coast to the northern Gulf of Alaska.

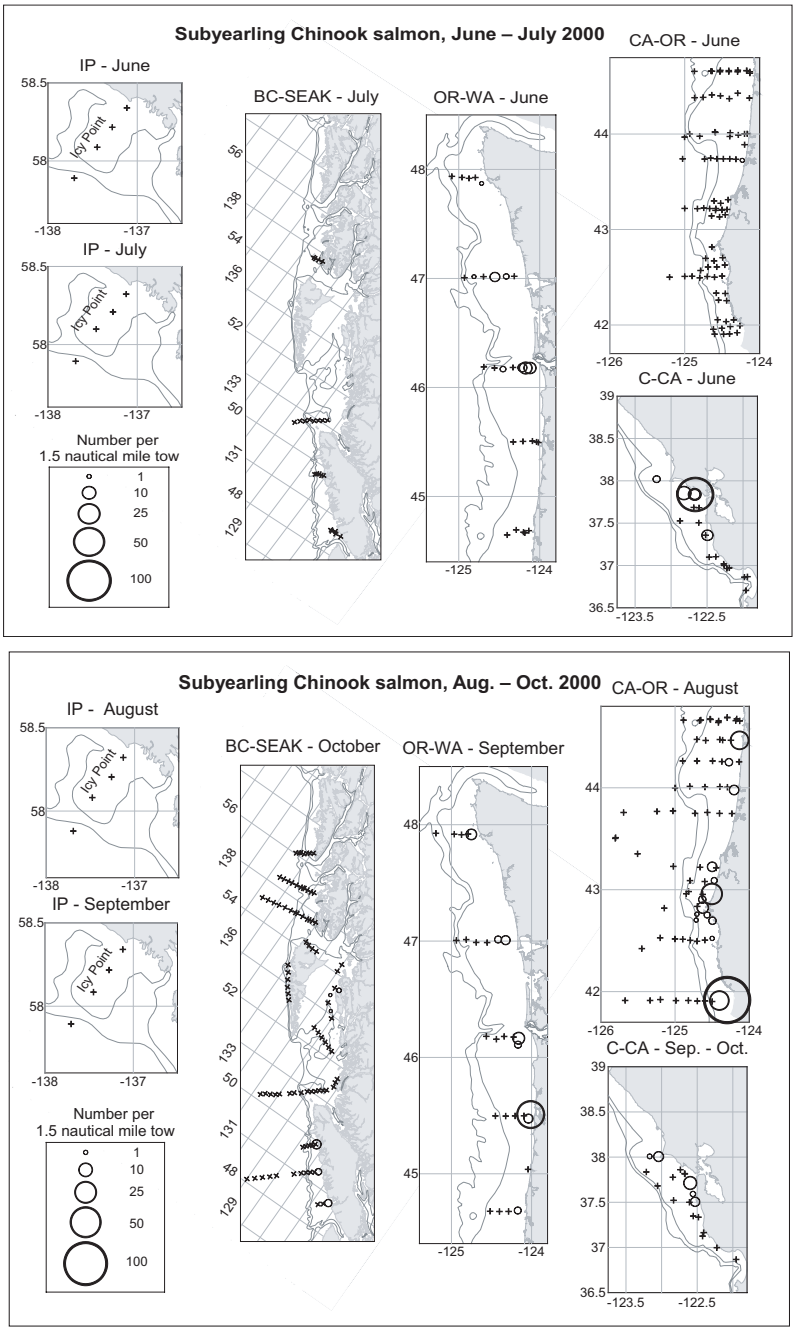
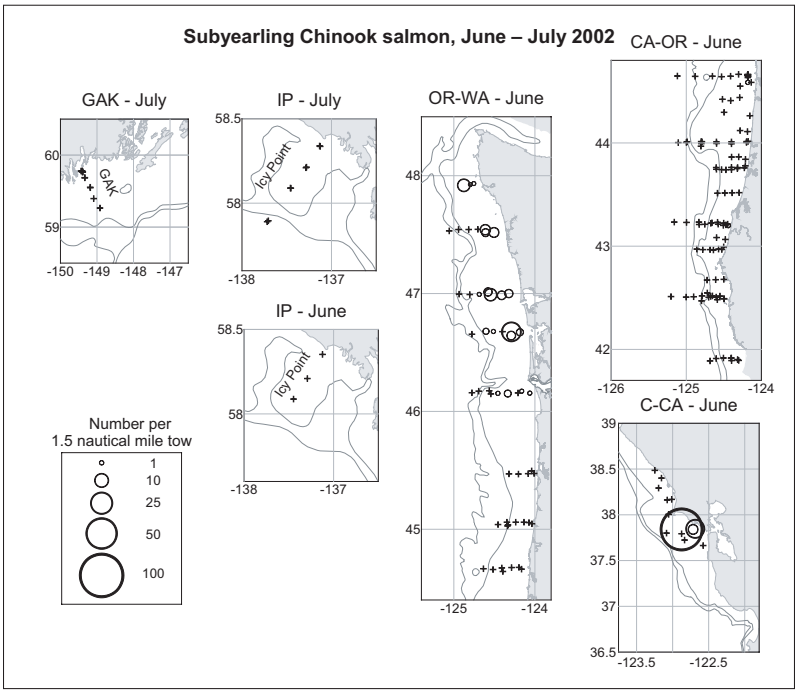


Figure A1. CPUE (number × 1.5 nmi towed^{-1}) of subyearling Chinook salmon in 2000 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 116 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.



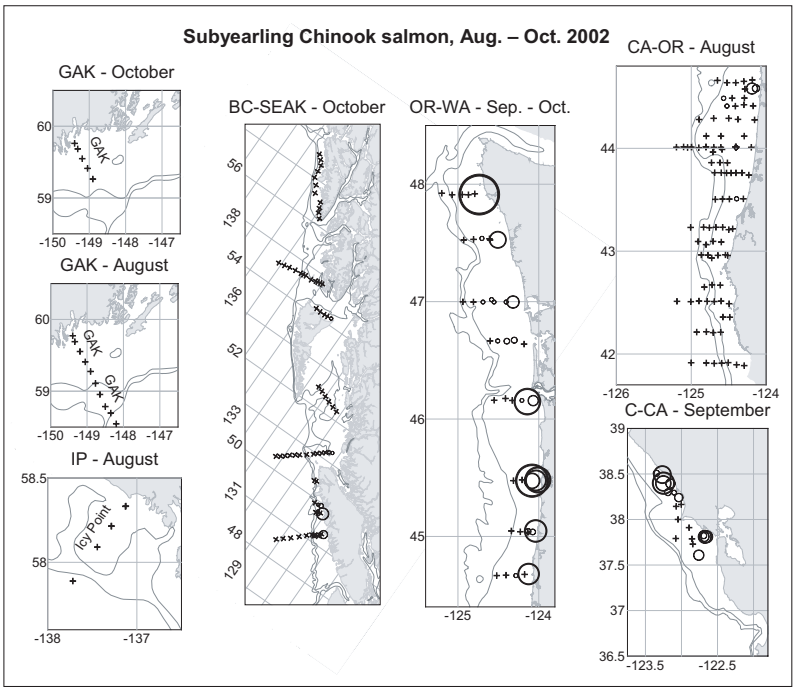


Figure A2. CPUE (number × 1.5 nmi towed^{-1}) of subyearling Chinook salmon in 2002 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

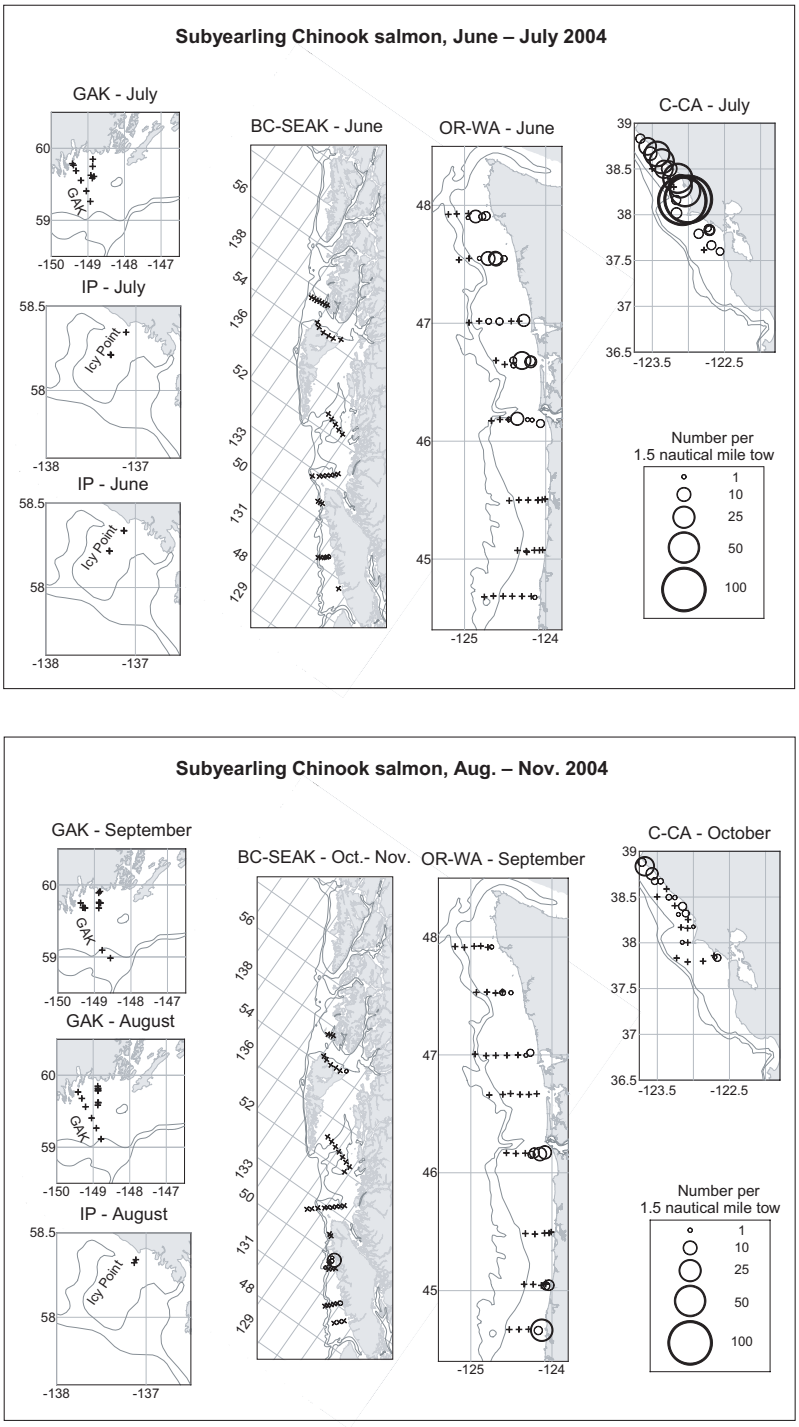


Figure A3. CPUE (number × 1.5 nmi towed^{-1}) of subyearling Chinook salmon in 2004 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 123 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and August– November catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

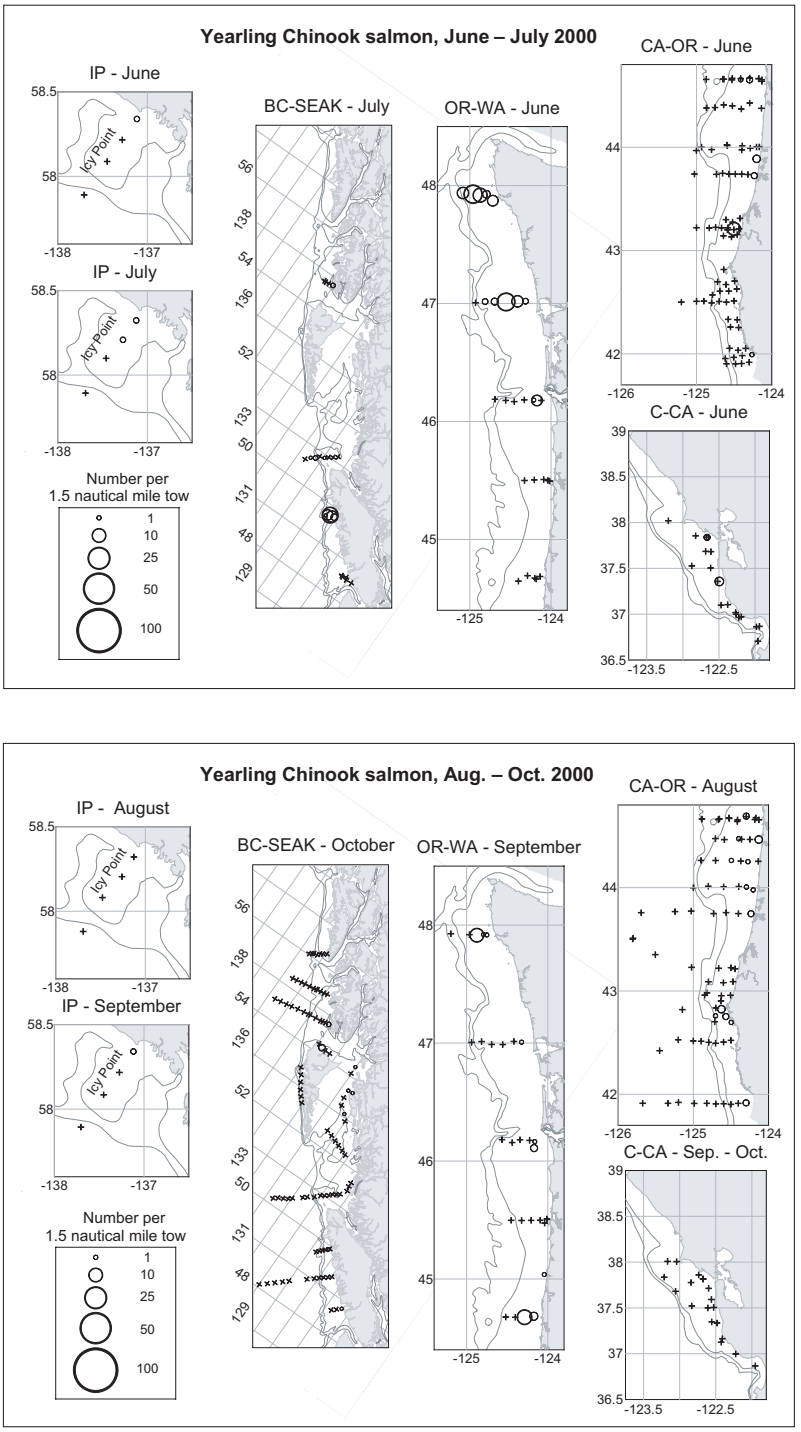
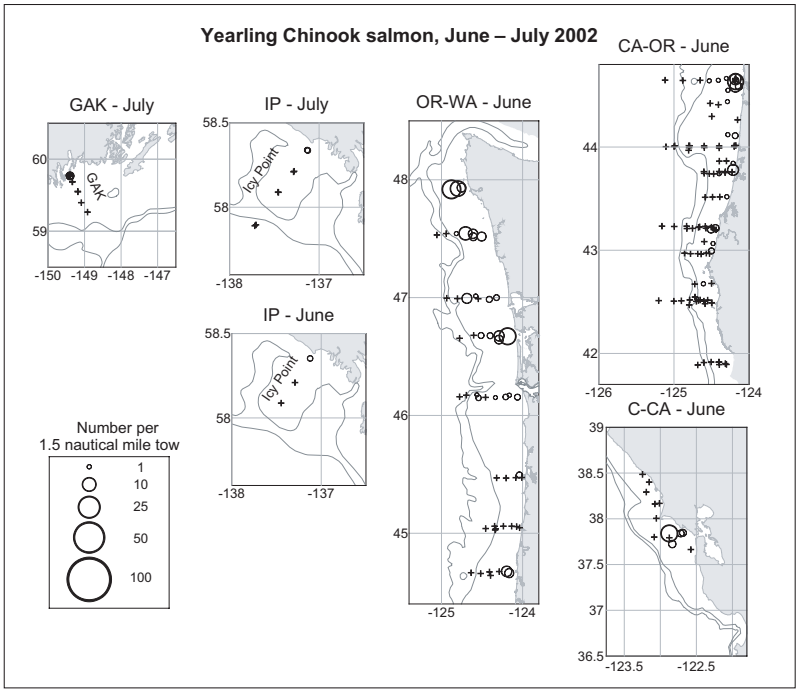


Figure A4. CPUE (number × 1.5 nmi towed^{-1}) of yearling Chinook salmon in 2000 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.



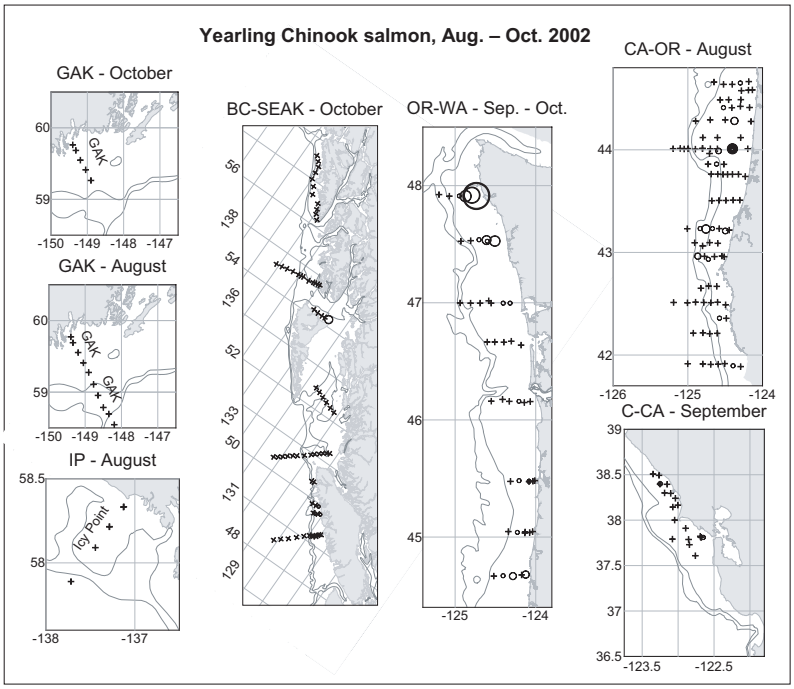
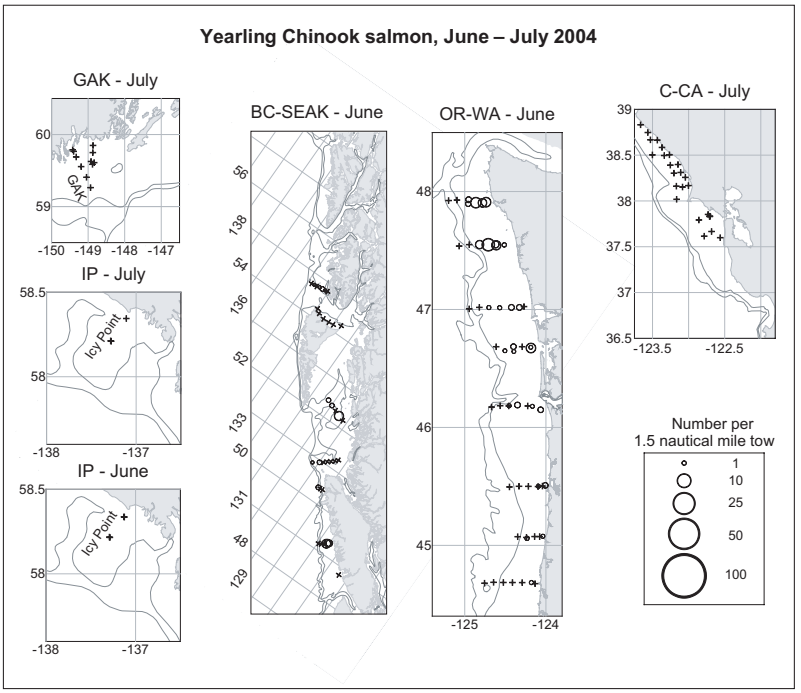


Figure A5. CPUE (number × 1.5 nmi towed^{-1}) of yearling Chinook salmon in 2002 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.



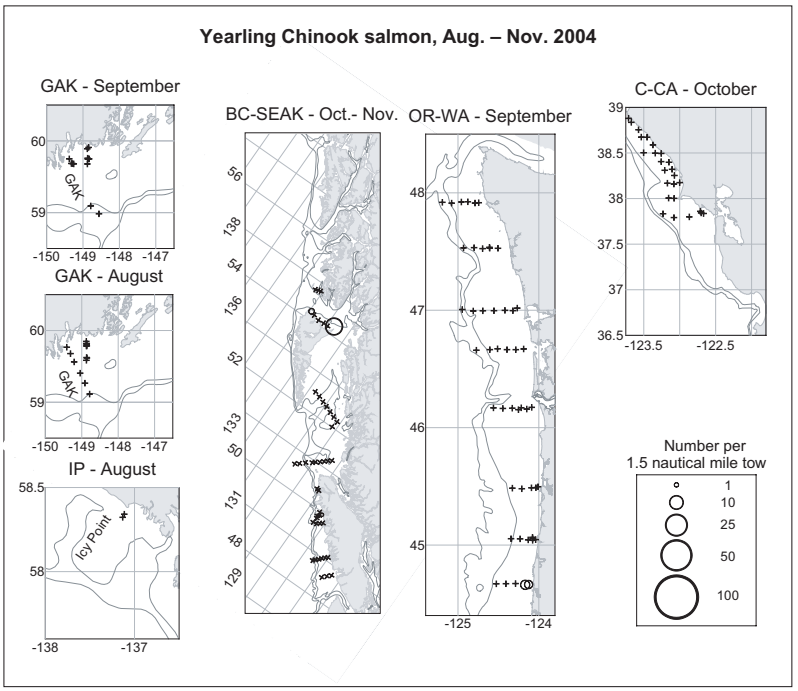


Figure A6. CPUE (number × 1.5 nmi towed^{-1}) of yearling Chinook salmon in 2004 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. Crosses represent 0 catch. June and July catches are shown in the top panel and August–November catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

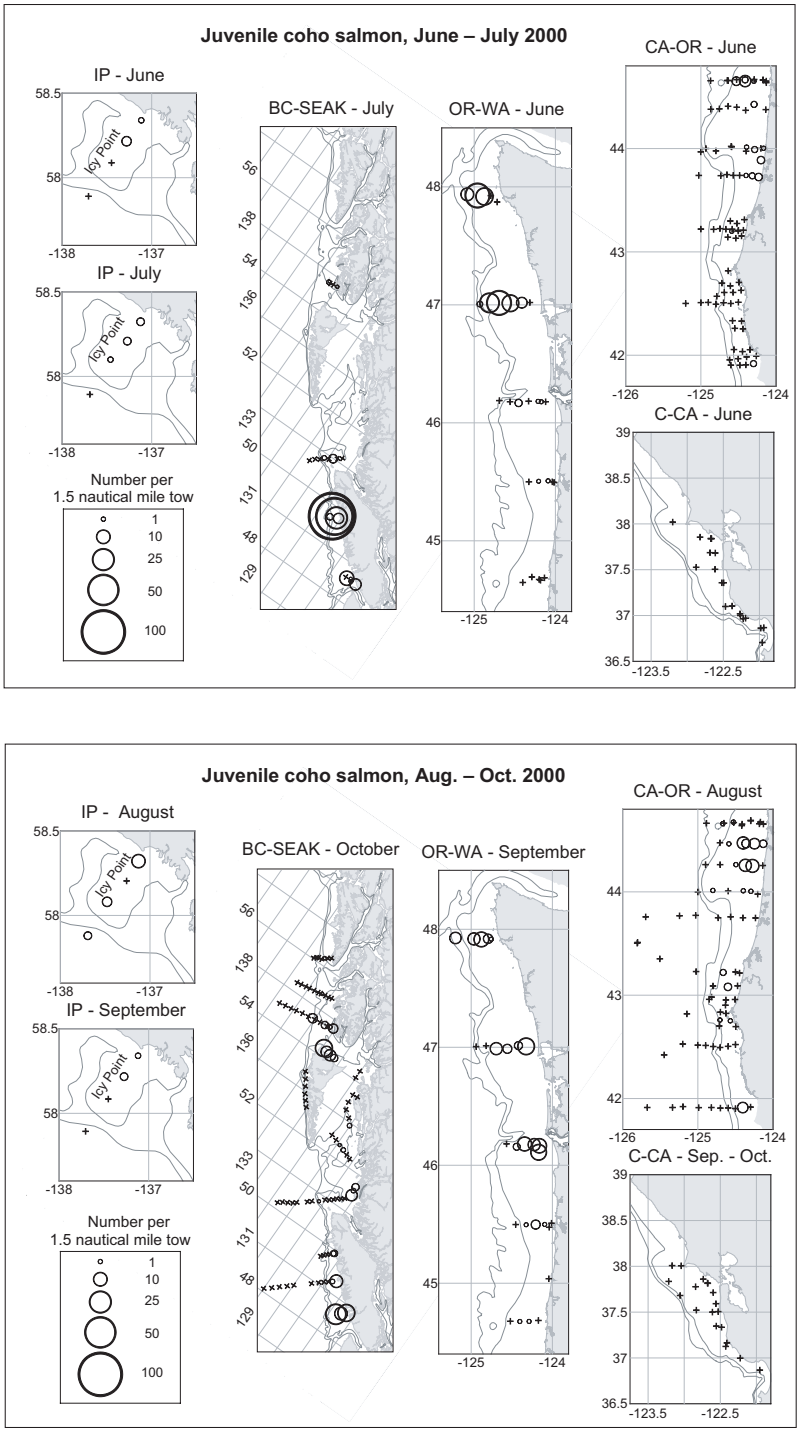
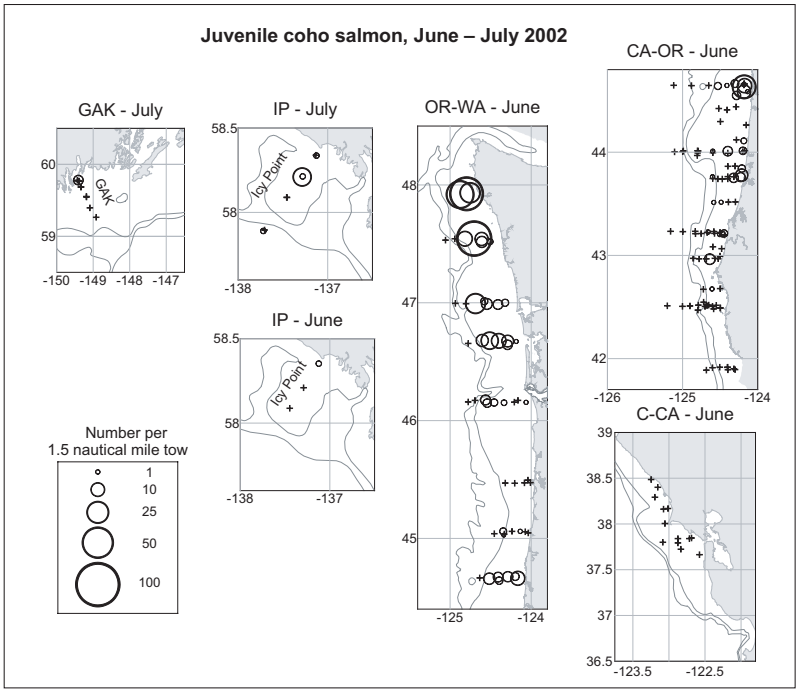


Figure A7. CPUE (number × 1.5 nmi towed^{-1}) of juvenile coho salmon in 2000 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 115 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.



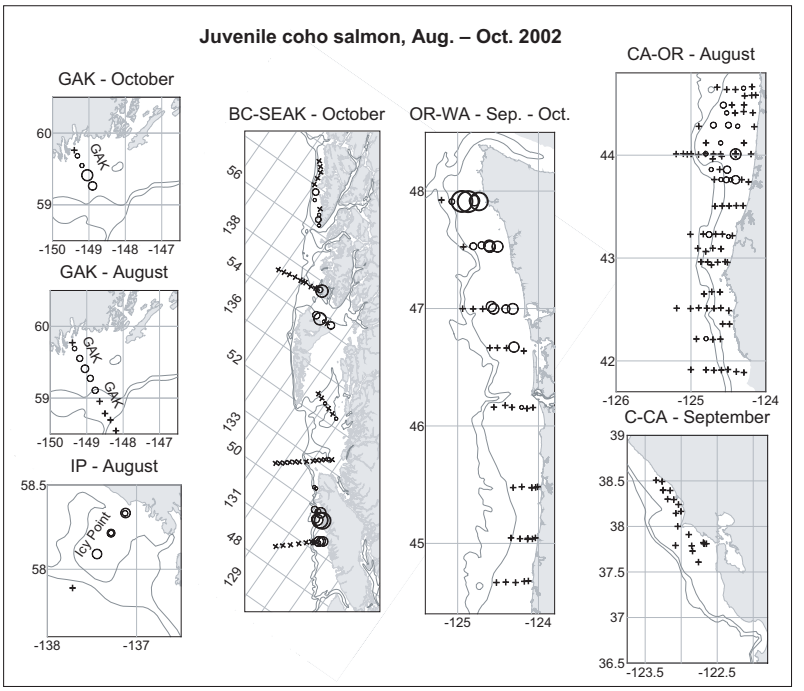


Figure A8. CPUE (number × 1.5 nmi towed^{-1}) of juvenile coho salmon in 2002 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

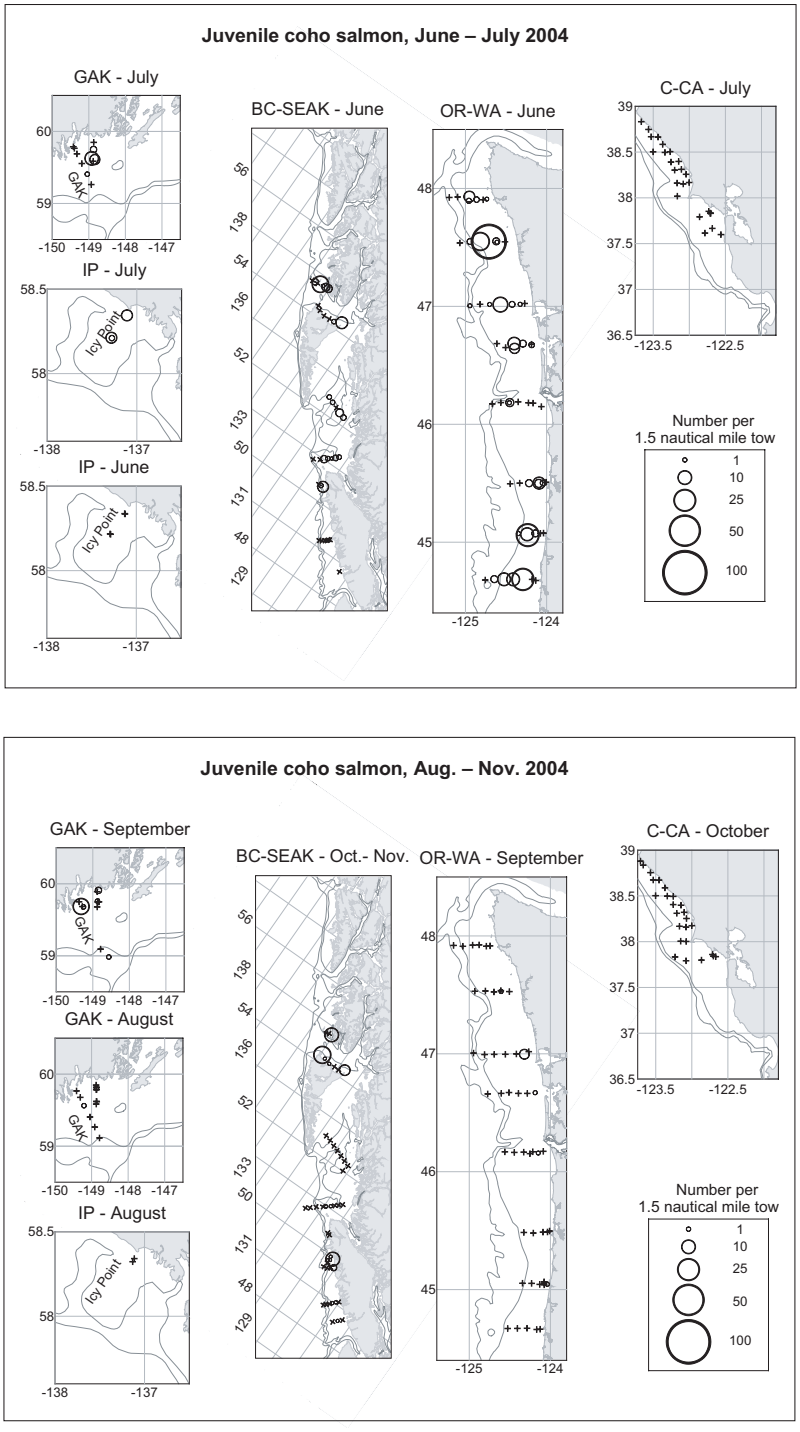


Figure A9. CPUE (number × 1.5 nmi towed^{-1}) of juvenile coho salmon in 2004 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. Crosses represent 0 catch. June and July catches are shown in the top panel and August–November catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

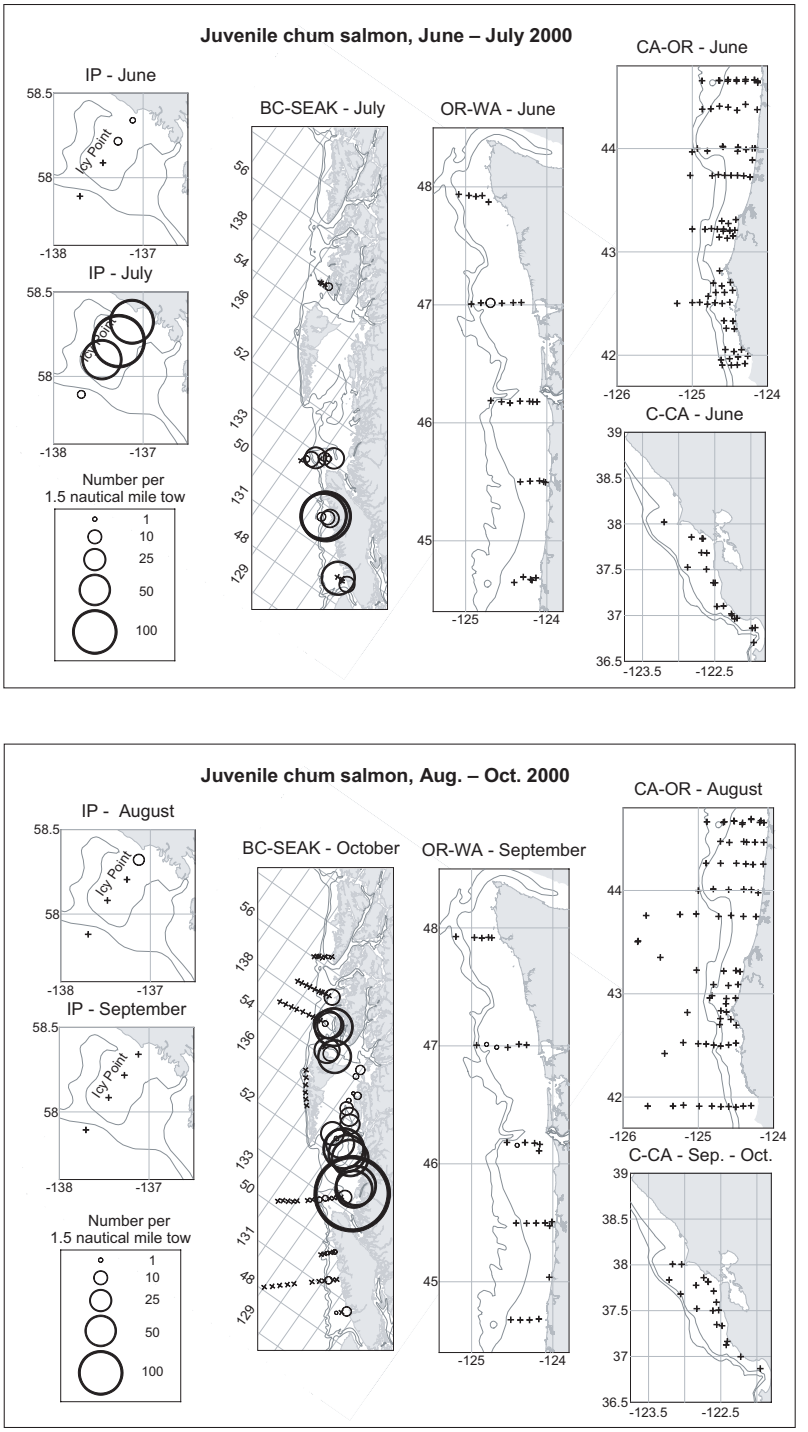


Figure A10. CPUE (number × 1.5 nmi towed^{-1}) of juvenile chum salmon in 2000 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 295 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

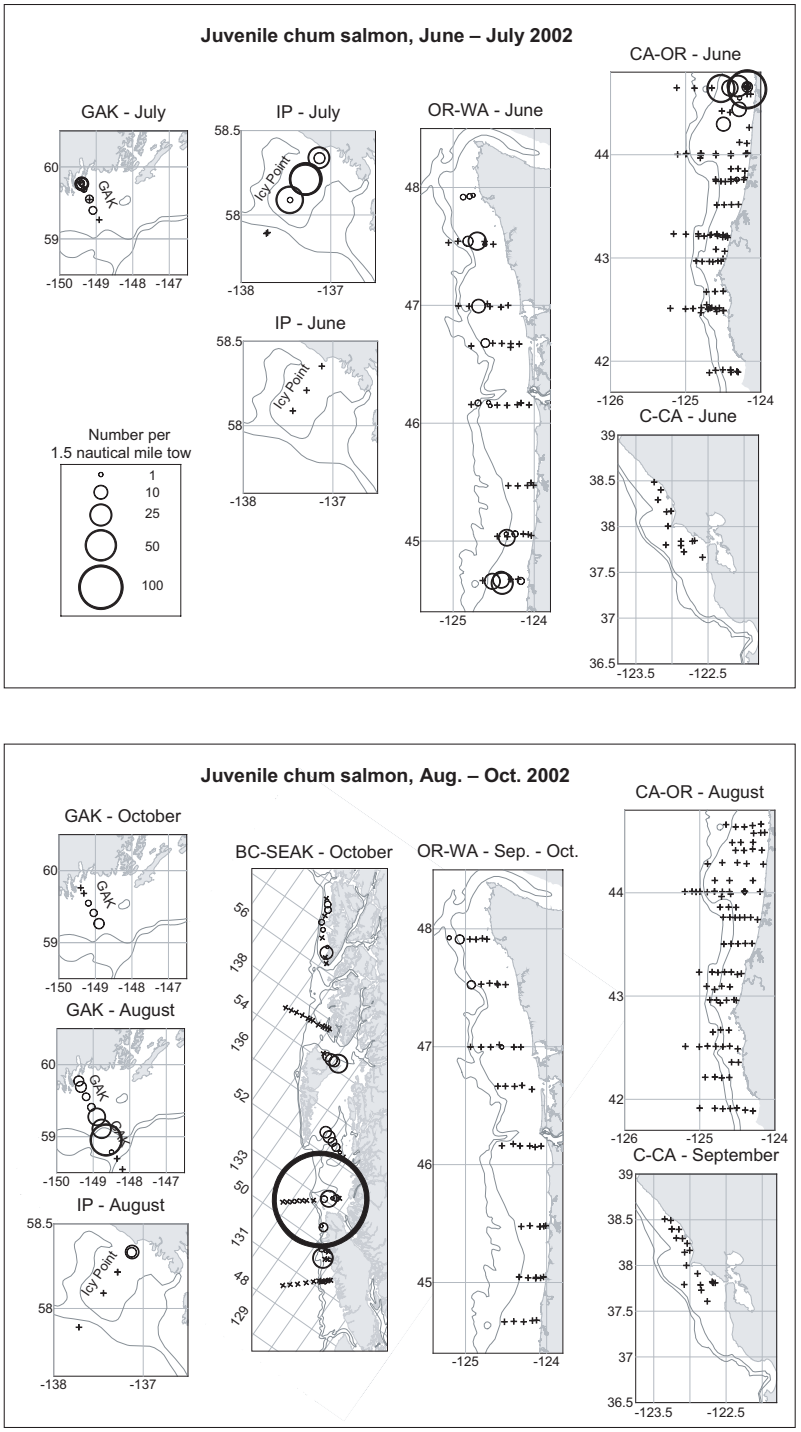


Figure A11. CPUE (number × 1.5 nmi towed^{-1}) of juvenile chum salmon in 2002 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 470 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and Aug–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

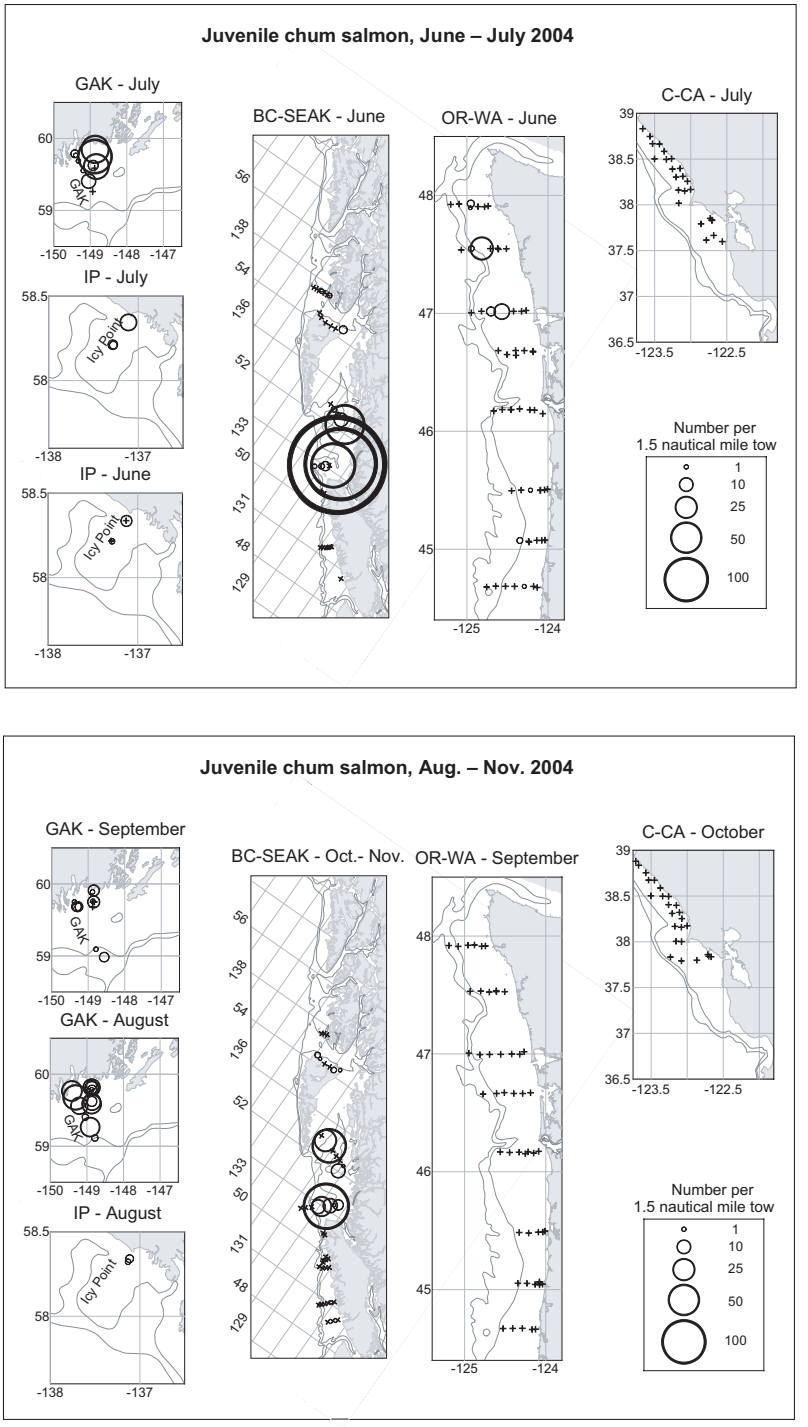


Figure A12. CPUE (number × 1.5 nmi towed^{-1}) of juvenile chum salmon in 2004 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 498 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and August–November catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

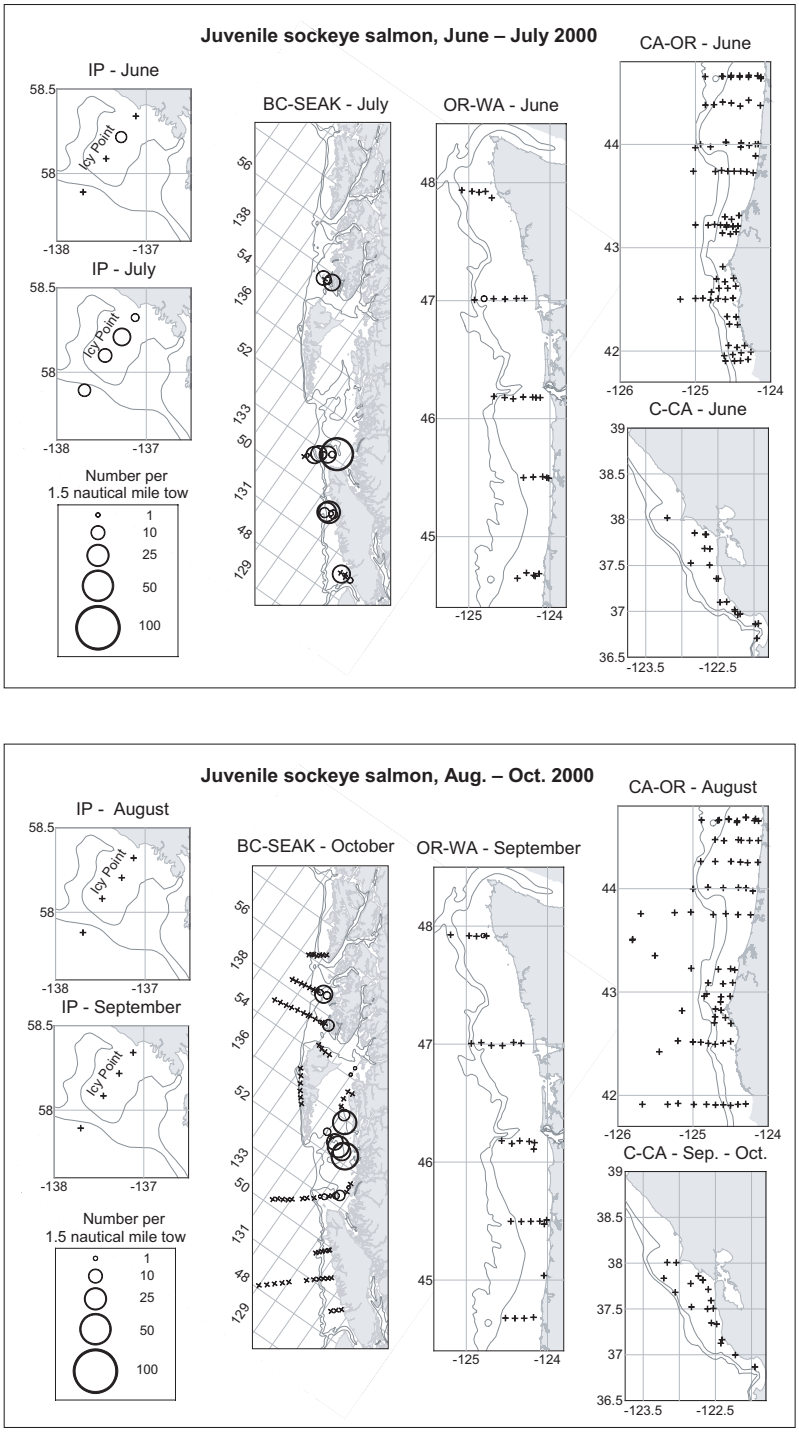


Figure A13. CPUE (number × 1.5 nmi towed^{-1}) of juvenile sockeye salmon in 2000 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

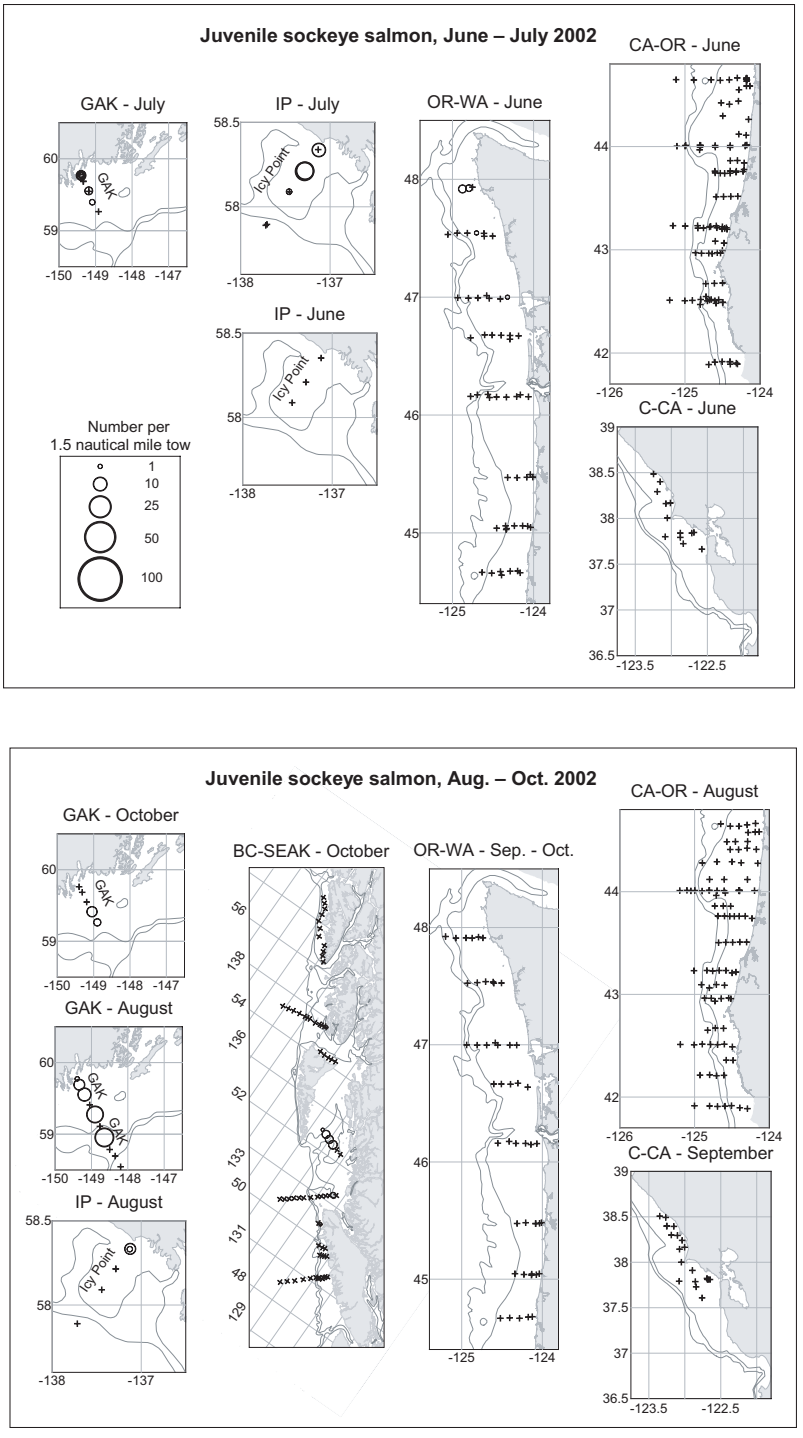


Figure A14. CPUE (number × 1.5 nmi towed^{-1}) of juvenile sockeye salmon in 2002 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

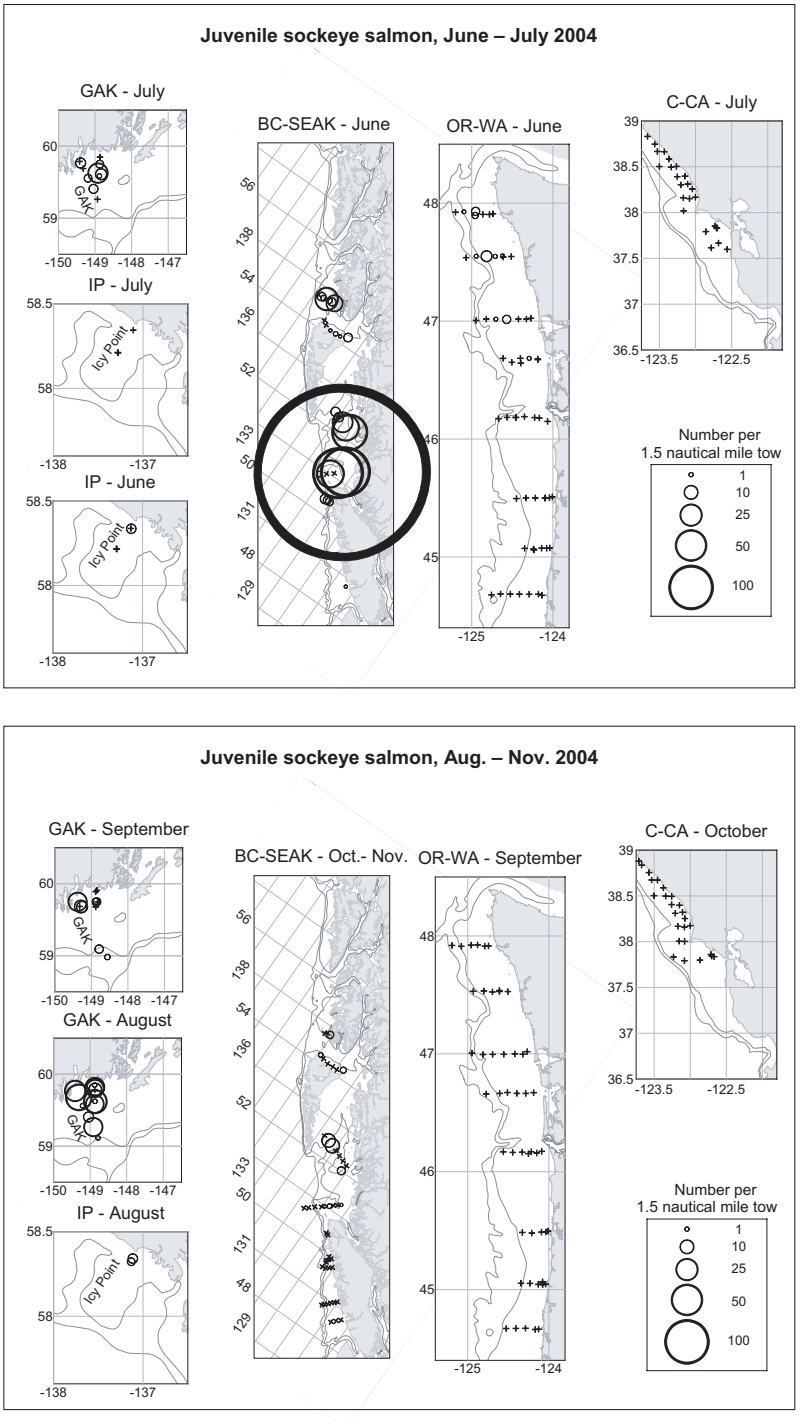


Figure A15. CPUE (number × 1.5 nmi towed^{-1}) of juvenile sockeye salmon in 2004 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 1,562 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and August–November catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

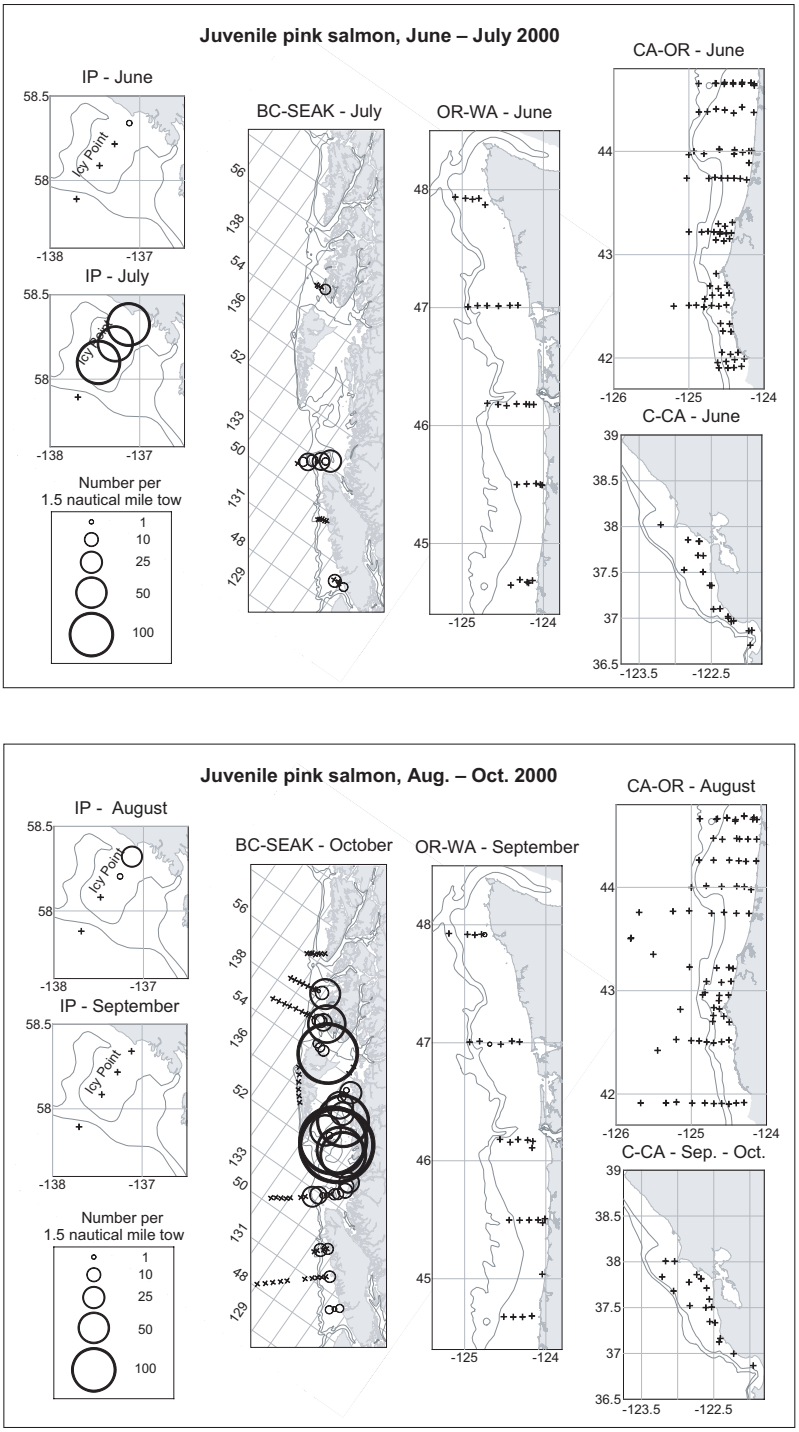
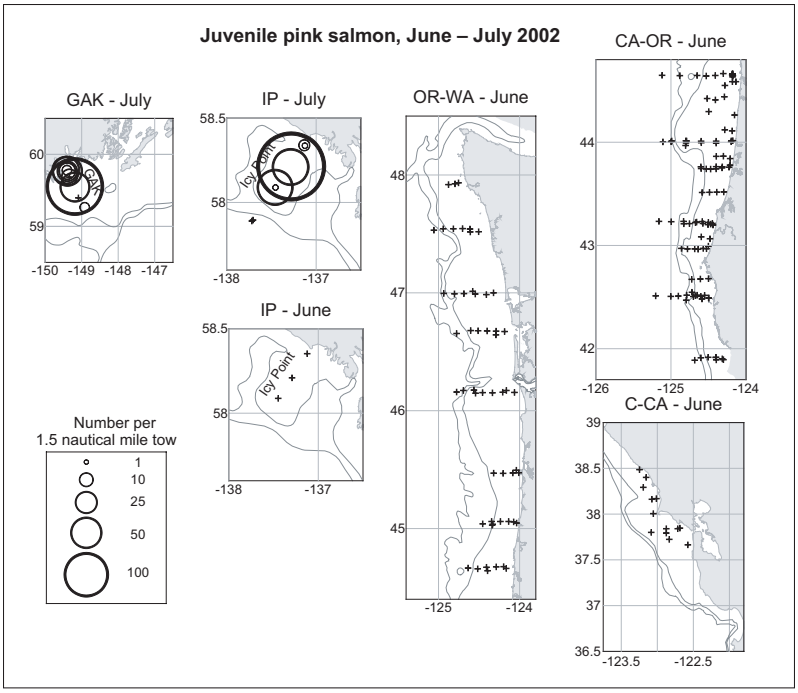


Figure A16. CPUE (number × 1.5 nmi towed^{-1}) of juvenile pink salmon in 2000 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 294 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.



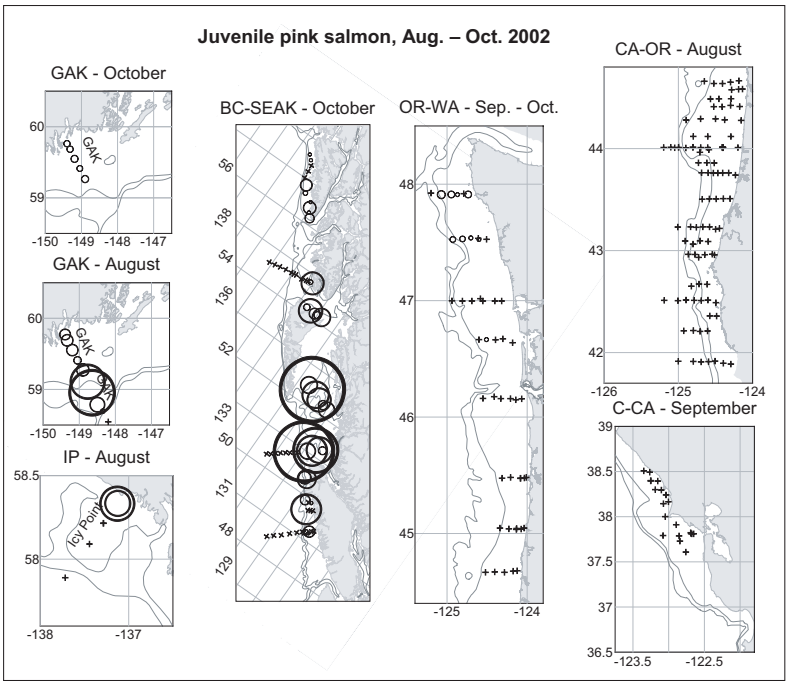


Figure A17. CPUE (number × 1.5 nmi towed^{-1}) of juvenile pink salmon in 2002 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 239 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and August–October catches in the bottom panel. The 200-m and 500-m isobaths are indicated.

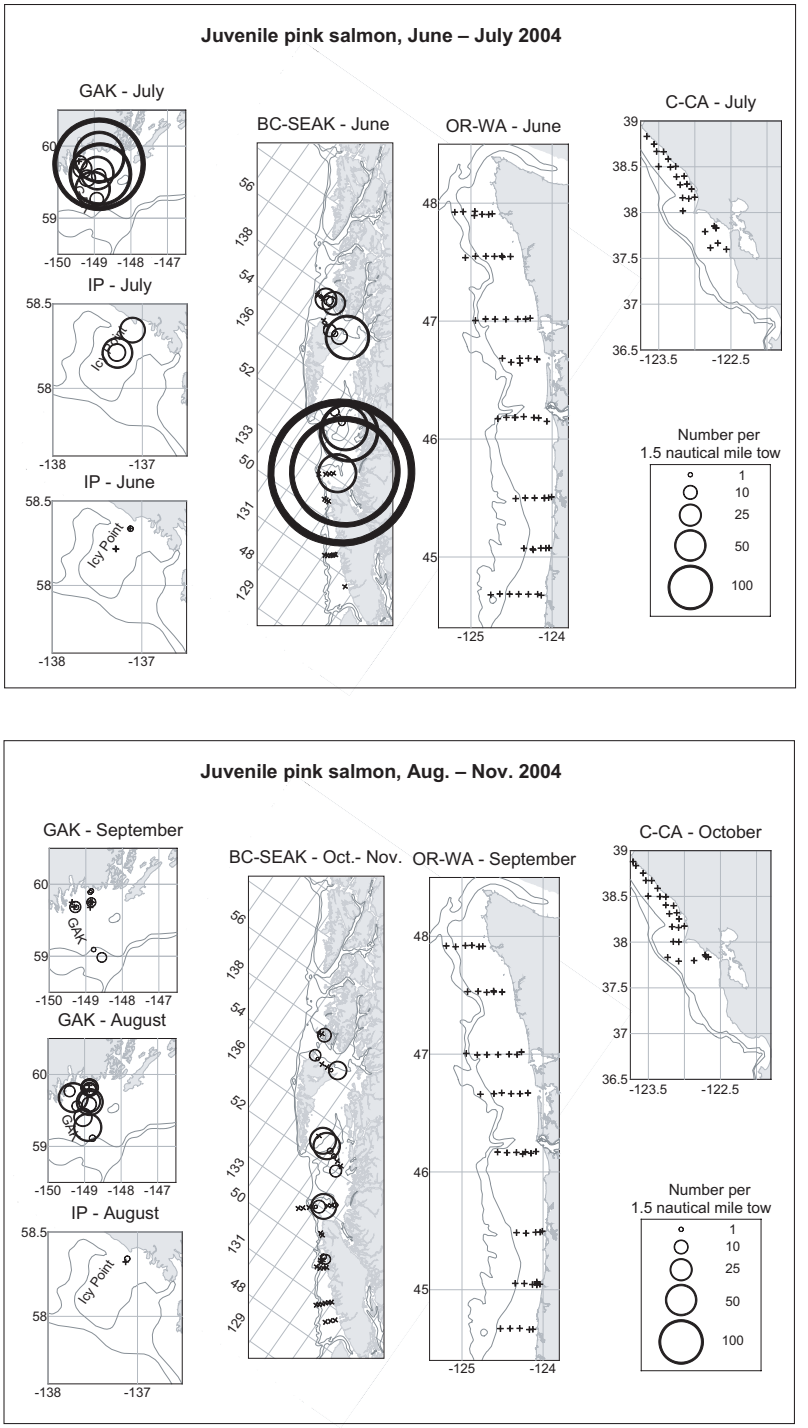


Figure A18. CPUE (number × 1.5 nmi towed^{-1}) of juvenile pink salmon in 2004 by month, region, and haul. Areas of circles vary continuously and are directly proportional to CPUE. The highest standardized catch was 1,083 fish. Crosses represent 0 catch. June and July catches are shown in the top panel and August–November catches in the bottom panel. The 200-m and 500-m isobaths are indicated.