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Spatio-Temporal Variation in Vertical Distributions of Pacific Salmon in the Ocean

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Abstract: The vertical distribution of Pacific salmon (*Oncorhynchus* spp.) is of interest to biologists and the fishing industry. An understanding of the normal vertical distribution and movement of salmon facilitates better management of both directed and non-salmon fisheries and better evaluation of research data. Salmon vertical distribution can vary spatially in relation to distance from shore, depth of the water column, and by ocean region, and temporally by life-history stage, season, time of day, and ocean conditions. In coastal waters, juvenile salmon were usually less than 15 m from the surface. In offshore waters, salmon were usually within the top 40 to 60 m, above the thermocline, but occasionally were found from 80 to 120 m. They usually were near the surface at night, and moved vertically during the day. Sockeye salmon displayed the shallowest vertical distribution, followed by pink, coho, chum, and Chinook salmon. There are limited data for winter, but vertical distributions may not change substantially from summer in offshore waters, while it may shift in some species in coastal and shelf areas. There is a need for more long-term data, throughout the marine residency of individual fish.

Keywords: Pacific salmon, vertical distribution, depth, diel behavior, data storage tags

INTRODUCTION

The depths to which Pacific salmon (*Oncorhynchus* spp.) dive has long been of interest to biologists and the fishing industry. It is important to understand the normal vertical distribution and movement of salmon for a number of reasons. Non-salmon fisheries may be better managed to avoid salmon by-catch if salmon vertical distribution and behavior are known. Also, the effect of changes in ocean and climate conditions on salmon distribution and abundance may be more accurately assessed. Salmon surveys may be better planned and survey data can be better evaluated if vertical distribution information is used when considering time of sampling, season, depth of gear, region surveyed, and age and species of salmon.

Salmon vertical distribution may vary spatially for a number of reasons, including distance from shore, depth of the water column, and ocean region. It may also vary temporally as a function of life-history stage, season, time of day, and ocean conditions.

Fisheries scientists have used a number of different methods and equipment to explore the depths at which salmon may be found. These include gillnets (Manzer 1964; Machidori 1966; French et al. 1971; Straty 1974; Pearcy and Fisher 1988), longlines (Godfrey et al. 1975), trawls (Ueno 1992, 1994; Erickson and Pikitch 1994; Radchenko and Glebov 1997, 1998), trolling (Beacham 1986; Orsi and Wertheimer 1995), hydroacoustics (Nero and Huster 1996; Sakai et al. 1997), ultrasonic and radio tags (Quinn 1988; Quinn et al. 1989, Ruggerone et al. 1990; Ogura and Ishida 1992, 1995; Ogura 1999), and archival data tags (Wada and Ueno 1999; Tanaka et al. 2000, 2001; Walker et al. 2000; Ishida et al. 2001; Murphy and Heard 2001, 2002; Azumaya and Ishida 2005; Tanaka et al. 2005). There are limitations for all these types of gear that may lead to biases in the results.

Here we present new data from trawl surveys, bycatches and data storage tags, and review and compare previously published information on salmon swimming depths.

MATERIALS AND METHODS

24-Hour Trawl Observations

In 2003 and 2004, scientists aboard the Russian research

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vessel *TINRO* conducted trawls throughout 24-h periods in August and September in the Aleutian Basin of the Bering Sea at 58°N, 172°E. Trawl surveys were conducted using a midwater rope trawl (40 m vertical opening; 30 m long; trawl opening perimeter 396 m; headrope length 80 m; four bridles 100–120 m long; warp lengths 245–280 m) towed for one hour. In 2004, over a 14-day period the trawl was set every four hours such that the headrope was at nine different levels on successive hauls: 0, 40, 80, 120, 160, 200, 350, 500, and 750 m. Depths were verified by acoustic readings. Each stratum was sampled seven times (Glebov et al. 2005). In 2003 the sampling was conducted at 0, 30 and 60 m over three days. The number of each species caught at each depth was counted and expanded to an index of abundance (number per cubic kilometer) using a formula based on catch of a species, weight of that species in the catch, size of the opening of the trawl, trawl speed and duration, and a fishing efficiency coefficient (0.3 for salmon longer than 30 cm, 0.4 for those shorter than 30 cm) (Sviridov et al. 2003).

Trawl Bycatch Data Analysis

A data set of information on Chinook salmon (*O. tshawytscha*) caught incidentally in eastern Bering Sea trawl fisheries from 1997 to 2000 was examined. Fishing depth (as determined by fishermen using various instrumentation and reported in logbooks) was used as the depth at which Chinook occurred. Data on depth of capture were stratified into month and ocean age (number of winters spent at sea) of the fish. Age and depth information were available for 5,246 fish. Most of the data were collected in January–February (48%) and September–October (45%).

Information from Data Storage Tags

Data from several types of data storage tags (DSTs) were summarized. Tags recording pressure (converted to depth data) were deployed from research vessels from 1999 to 2005 and recovered in those years. Tags included models RL-41 and RL-42, manufactured by Conservation Devices, Inc., and refinements of these tags manufactured by Lotek Marine Technologies, models LTD_1100-300 and LTD_1100-500. DST CTD tags manufactured by StarOddi were also used. CDI and Lotek tags had depth resolutions of 1 or 2 m. StarOddi tags had a resolution of 0.15 m.

Fish were captured for tagging by research longline, hook-and-line, and trawl on Japanese and U.S. research vessels. Tags were attached to fish just anterior to the dorsal fin using two nickel pins, with labeled disk tags placed on the pins on the other side of the fish. DST CTD tags were attached in the same location and with the same method, but were affixed with stainless steel wire, with a small oval plastic plate on the opposite side of the fish.

In the initial period after tagging, salmon sometimes remained near the surface for several days to more than a week, probably due to trauma from tagging (Walker et al. 2000). Data from this period were considered abnormal and were excluded. As chum salmon (*O. keta*) approach coastal areas on their homeward migration, they sometimes dive to great depths (> 200 m; Ueno 1992, 1994; Wada and Ueno 1999; Azumaya and Ishida 2005). These data were included in calculations of depth distributions.

Day and night periods were estimated from times of sunrise and sunset at release and recovery locations on the days a fish was tagged and recovered. A linear interpolation

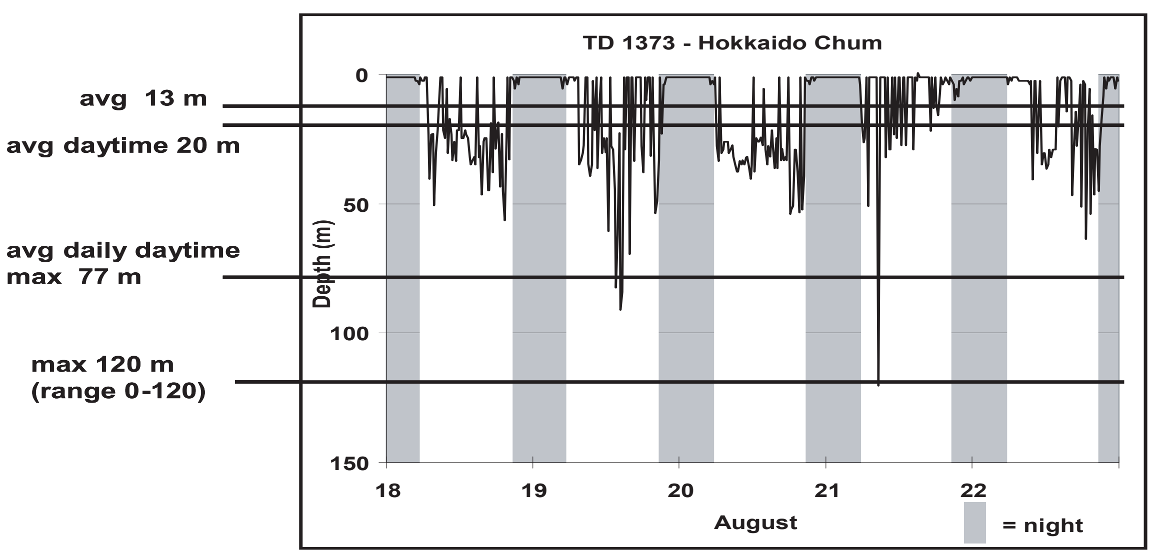

Fig. 1. Example of differences in calculations of average (daily) depth, average daytime depth, average daily maximum depth, and maximum depth. Data from a 5-day period recorded on temperature-depth data tag TD 1373 during homeward migration of a chum salmon returning to Hokkaido, Japan, from the Bering Sea in 2002.

was made between these endpoint values, producing a 'sunrise' and 'sunset' value at each data point recorded. Each data point also had an actual time of day recorded by the tag. The actual times were tested against the estimated times of sunrise and sunset at that point, and if the actual time was between the estimated sunrise and sunset, that point was characterized as a daytime value. Because day and night characterizations were estimated, fits with actual local diurnal cycles were not likely to be completely accurate. This would lead to some daytime data points being incorrectly characterized as nighttime, and vice versa. Thus the day/night differences we report are most likely smaller than they actually were.

In addition to calculating average depths, average 'maximum' depths were also calculated. This entailed finding the maximum depth recorded for each day (24 h), daylight, or nighttime period, and averaging these maximum depths (Fig. 1). Average daily minimum depths were also calculated.

RESULTS

24-Hour Trawl Experiments

In 2004, only immature (as assessed by gonad weight-body weight indices) chum salmon were taken in appreciable numbers (2.4% of immature chum captured) at depths other than 0 to 40 m (Table 1). Other species and maturity groups (maturing chum, juvenile (as estimated from body length) and maturing coho, *O. kisutch*) were taken only in the 0–40 m layer, except for a few immature sockeye (*O. nerka*) (40 to 80 m in the afternoon) and immature Chinook salmon (120 to 160 m at noon). It is likely that the rare catches of immature chum salmon at deep strata were artificial and were taken at shallower depth during the process of setting and retrieving the trawl. The decrease of chum salmon CPUE in the 0–40 m layer in evening, with no simultaneous significant increase of CPUE in deeper water layers, is likely attributable to migration within the upper 40 m to a level very near

Table 1. Estimated abundance of salmon (fish/cubic km) in diurnal trawl experiments at 6 depth strata within the Aleutian Basin, western Bering Sea (58°N, 172°E) from 23 August to 5 September, 2004. Im = immature; Mat = maturing; Juv = juvenile.

Depth (m)	Species	Morning	Noon	Afternoon	Evening	Midnight	Late night
0–40	Im chum	46,638	49,387	72,759	17,273	44,902	42,494
	Im sockeye	12,823	17,261	25,346	1,678	13,764	11,414
	Im Chinook	798	1,307	1,059	987	2,156	2,870
	Juv coho	66	0	91	219	110	189
	Mat chum	165	0	258	89	0	615
	Mat coho	91	0	0	83	0	0
40–80	Im chum	313	466	1,240	0	0	1,627
	Im sockeye	0	0.0	310	0	0	0
80–120	Im chum	0	2,295	0	0	0	0
	Im Chinook	0	156	0	0	0	0
350–390	Im chum	0	296	0	0	0	0
500–540	Im chum	281	0	0	0	0	0
750–790	Im chum	0	313	0	0	0	0

Table 2. Estimated abundance of salmon species (fish/cubic km) in diurnal trawl experiments within three depth strata within the Aleutian Basin, western Bering Sea (58°N, 172°E) during 8–10 September, 2003. Im = immature; Mat = maturing; Juv = juvenile. Times of day represent 6 sets of tows conducted 4 hours apart.

Depth (m)	Species	Morning	Noon	Afternoon	Evening	Midnight	Late night
0–30	Im chum	12,096	51,672	56,999	71,102	69,971	47,348
	Im sockeye	3,122	4,665	4,324	3,878	9,426	12,522
	Im Chinook	780	1,435	1,572	1,300	2,175	0
	Juv coho	0	0	294.8	141.4	544	0
	Mat chum	390	359	786	734	1,088	0
60–90	Im chum	303	1,827	2,768	1,204	156	293
	Im sockeye	0	609	0	301	0	293
	Im Chinook	303	0	308	0	0	0
90–120	Im sockeye	0	290	0	0	0	0

Table 3. Average depth in meters of bycatch of Chinook salmon in eastern Bering Sea trawl fisheries (1997–1999), tabulated into ocean age (winters spent at sea; all freshwater ages are combined, and represented by the dash preceding the period). Percentage of catch within 25-m depth intervals is also presented.

	January–February						September–October				
Ocean age (yrs)	-.1	-.2	-.3	-.4	-.5	All ages	-.1	-.2	-.3	-.4	All ages
N	39	279	1,317	798	82	2,515	368	1,455	497	20	2,340
Avg. depth (m)	58.1	107.8	65.9	51.2	47.7	65.2	80.8	78.1	69.6	63.0	76.6
25m depths	%										
0		0.7	1.9	2.5	1.2	1.9	0.0	0.0			
25	79.5	41.6	55.0	62.9	72.0	56.9	33.4	18.6	23.5	30.0	22.1
50	10.3	21.9	29.7	29.6	24.4	28.3	20.4	35.6	45.9	50.0	35.5
75		3.6	2.3	0.9		1.9	15.8	22.5	16.5	15.0	20.1
100		2.2	0.5			0.5	11.4	12.4	7.4		11.1
125	2.6	0.7	0.5	0.3		0.4	9.5	6.9	3.8	5.0	6.6
150			0.3	0.1		0.2	6.8	3.2	2.2		3.5
175		2.2	1.3	0.4		1.0	1.9	0.9	0.6		1.0
200	5.1	5.0	1.5	1.5		1.9	0.5				0.1
225		5.4	3.1	0.9	1.2	2.5					
250	2.6	9.7	2.6	0.4		2.6	0.3				0.0
275		6.8	1.3	0.6	1.2	1.7					
300		0.4	0.2			0.1					

the surface, where the trawl may not fish effectively.

In the September 2003 diurnal experiments, nearly all salmon (mature chum, juvenile coho, and immature chum, sockeye, and Chinook salmon) were taken in the 0 to 30 m layer (Table 2). Immature chum salmon were also taken between 30 and 60 m throughout the 24-hr period. A few (3.8% of sockeye caught) immature sockeye salmon were taken at depth intervals 30 to 60 m and 60 to 90 m, and a few (7.8%) immature Chinook salmon at 30 to 60 m. While the net opening was not closed during set and retrieval, for the great majority of the time the net fished at the targeted depth. While a few fish may have been caught during set or retrieval, the fact that almost all salmon were caught in the top (0–40 m) interval demonstrates that few fish are taken during ascent or descent to deeper depths.

Trawl Bycatch Data Analysis

Eastern Bering Sea groundfish trawl bycatch of Chinook salmon included more older fish in winter (87% ocean age -.3 and older) and more younger fish in summer–fall (78% ocean age -.1 and -.2). Over 90% were caught between 25 m and 175 m; less than 3% were deeper than 300 m. Chinook were slightly deeper in autumn (77 m average fishing depth in September–October, vs. 65 m January–February), and younger fish tended to be slightly deeper than older fish (Table 3). Depth distribution showed a bimodal tendency in winter, with the bulk of fish at 25–75 m and a smaller peak at 200–300 m.

Although groundfish trawling was not conducted to catch salmon or carried out according to any systematic or experimental design, the large quantity of data provided by the fishery gives a good picture of Chinook vertical distribution during the fishery. Similar trawl data from the U.S. West coast yielded important information on Chinook depth distribution and seasonal changes (Erickson and Pikitch 1994). The insights on changes in age distribution and at what depths Chinook salmon are most likely to be found can provide valuable guidance to managers and fishermen.

Data Storage Tag Experiments

Depth data from a limited number of DSTs (n = 38) confirm that Chinook and chum salmon had the deepest vertical distributions. Average depths (Chinook: 42 m; chum: 16 m) and average daily maxima (Chinook: 130 m; chum: 58 m) were deeper than those of the other three species (Table 4). Among sockeye, pink (*O. gorbuscha*), and coho salmon, sockeye had the shallowest vertical distribution (average 3 m, average daily max 19 m), followed by pink (average 10 m, average daily max 37 m) and coho (average 11 m, average daily max 46 m). Maximum depths recorded from any tag were 83 m for sockeye, 74 m for pink, 97 m for coho, 253 m for chum, and 344 m for Chinook (the maximum depth

Table 4. Recorded depths, in meters, of 5 salmon species based on information from data storage tags recovered in the North Pacific Ocean from 1999 to 2006. N= sample size, Avg = average depth, Min = minimum depth, Max= maximum depth.

Species	N	Avg Depth	Avg Daily Min	Avg Night	Avg Day	Day-Night Difference	Avg Night Max	Avg Day Max	Avg Daily Max	Max
Sockeye	12	3	0	3	4	1	9	18	19	83
Pink	3	10	1	4	13	9	19	36	37	74
Coho	10	11	0	8	12	4	29	42	46	97
Chum	11	16	1	8	20	12	33	56	58	253
Chinook	2	42	17	40	43	3	84	125	130	344

the tag was capable of recording). A nonparametric Dunn multiple comparison test of the means of average depths for the three species with more than three tags (sockeye n = 12, chum n = 11, coho n = 10) showed the differences between each pair of species were highly significant (sockeye-chum Q = 53.51; sockeye-coho Q = 26.98; coho-chum Q = 24.64; Dunn $Q_{0.001,3}$ = 3.588; Zar 1984). Comparison tests of the average daily maxima for these three species were also highly significant.

Most fish displayed a diel pattern of vertical distribution, moving between shallower and deeper waters during the day and near the surface at night (average nighttime depths of 3–8 m), except for Chinook salmon. The diel pattern was strongest in chum and pink salmon, and was variably expressed, even in a single fish. The Chinook data are from two fish, one tagged as an immature and the other as a maturing fish. The tag from the immature fish had two years of data showing several different patterns of vertical distribution that changed seasonally; the fish remained below 100 m for one winter. Data from all other fish are from maturing fish in summer and fall.

DISCUSSION

During the marine phase of their life history, most Pacific salmon enter coastal waters, move offshore as they become larger, and move through coastal waters again as they return to their natal rivers. Some stocks, for example coho and Chinook stocks of western North America, may remain near coastal areas throughout their life. Vertical distributions can vary with these three main marine stages.

Juvenile Salmon

Studies of juvenile salmon in coastal areas indicated that young fish were generally very near the surface. Straty (1974) found that outmigrating Bristol Bay sockeye were at about 1 m at night and 2 m during the day. Over half of juvenile Oregon coho were caught within the top 2 m (Pearcy and Fisher 1988). In September, 80–90% of southeastern Alaska coho and Chinook juveniles were caught within 30 m of the surface (Orsi and Wertheimer 1995). More than 95% of juvenile coho in the Strait of Georgia were caught within the top 45 m, 60–95% in < 15 m (Beamish et al. 2000). At a station sampled over a 24-h period 13 km southwest of the mouth of the Columbia River, most juvenile Chinook (89%) and coho (78%) salmon were in the top 12 m (Emmett et al. 2004).

Immature and Maturing Salmon in Offshore Waters

Orsi and Wertheimer (1995) found that larger Chinook juveniles could be caught at deeper depths, and deeper in fall than spring. This presages the greater depths at which immature and maturing salmon are found as they move to the wider offshore waters where they spend most of their lives and achieve the greater part of their growth. Manzer (1964) conducted some of the earliest investigations of salmon vertical distribution in offshore waters of the Gulf of Alaska in May–July. He found sockeye salmon mostly in the top 12 m at night and at 12 to 36 m during the day. Chum salmon were in the top 36 m at night and from the surface to over 60 m during the day. Both species were found to at least 60 m in May, but in June and July sockeye were limited to the top 36 m, possibly by the thermocline. There were no consistent differences by ocean age (-.2 and -.3) for either species. Few pink and coho salmon were caught, and both were "nearer the surface than sockeye and chum" (pink to 24–36 m; coho to 12–24 m).

In the western North Pacific, Machidori (1966) reported sockeye and chum salmon to be mostly in the top 20 m. French et al. (1971) caught sockeye, chum, pink, and coho salmon to 23 m (the deepest depth they fished) in spring and summer. Godfrey et al. (1975) reported most salmon were in the top 60 m, though a few coho and chum salmon were taken down to 80 m.

Tracking fish that carried ultrasonic tags allowed Ogura and Ishida (1992, 1995) and Ogura (1999) to gain insights into the detailed behavior of individual salmon in the central Bering Sea and North Pacific. Chum, pink, sockeye, coho, and Chinook salmon were all mostly within the top 50 m, and the first four species were primarily found shallower than 20 m. Chinook salmon were deeper (20–50 m) than other species. Coho salmon showed the clearest diurnal pattern of movement. Unfortunately, it was possible to track fish for only a few days (0.6 to 5.5 days).

Possible tagging or vessel effects may have obscured normal behavior.

The data we have presented on diel trawl surveys in the Bering Sea are consistent with these other findings. The great majority of fish caught were within the upper 40 m. Because the opening of the trawl is 40 m deep, finer resolution of vertical distribution was not possible.

There is very little winter data for vertical distribution of salmon in the open waters of the North Pacific and Bering Sea. Two hydroacoustic surveys in winter indicate that salmon of unidentified species in the open North Pacific were generally still within the top 40 m (Nero and Huster 1996; Sakai et al. 1997). Because salmon seem less abundant at night in these surveys, it may be concluded that they also continued their diurnal behavior pattern of vertical distribution and were near the surface (harder to detect with hydroacoustics) at night.

Data storage tags permit a longer-term look at what salmon do at sea. Nine tags on Japanese chum salmon also showed fish usually within the top 60 m, making deeper excursions during the day than at night (Wada and Ueno 1999; Azumaya and Ishida 2005; Tanaka et al. 2005). Depths over 80–100 m generally were not accessed until the fish neared Japan, when they occasionally descended to 150–360 m. These data are very similar to those we have retrieved from 11 data tags on chum salmon returning to Japan and Russia. The short intervals of data collection (every 5 s) on the tag analyzed by Tanaka et al. (2005) also allowed an accurate characterization of the daytime dives by chum salmon. They found fish made dives about 8.6 times per hour, with a duration of 5.1 min and 1.4-min intervals between dives. Fish were presumed to be feeding on prey which had moved deeper during daylight hours.

Immature and Maturing Salmon in Coastal Waters

Chinook salmon remaining in coastal waters throughout most of their lives may have different depth distributions. Data tags on Chinook in southeastern Alaska coastal waters showed several different diel patterns: no apparent pattern, nearer surface at night and deeper during the day, and deeper at night and nearer the surface during the day (Murphy and Heard 2001, 2002). Fish were generally within the top 60 m. Hinke et al. (2005) also found no consistent diel pattern, but discerned four different "habitats" or patterns of vertical distribution in data from 15 Chinook salmon off northern California and southern Oregon: a shallow night pattern around 10 m; a shallow day pattern at 0–80 m; a deep (mostly night) pattern around 55 m; and a deeper pattern around 100 m (60–280 m). Ocean age -.1 and -.2 Chinook salmon in southeastern Alaska were caught at deeper depths than juveniles (Orsi and Wertheimer 1995).

On the northeastern Bering Sea shelf, Russian trawl fisheries captured Chinook salmon incidentally at depths to 360 m throughout the year, and chum salmon in summer and fall (Radchenko and Glebov 1997, 1998). The majority (90%) of Chinook were taken from 50 to 400 m, and were taken from slightly deeper areas from August to September. As in our analysis of eastern Bering Sea trawl data, they found older fish were more numerous in winter and younger fish were more abundant in the summer and fall. Erickson and Pikitch (1994) analyzed bycatch of Chinook salmon in US West coast trawl fisheries. Bycatches were larger in winter and were in a greater depth range (100–482 m), than in summer (< 220 m).

There have been a number of studies that shed light on behavior of maturing salmon as they return to coastal areas prior to spawning. A Japanese chum salmon moving along the eastern edge of the Kuril Islands to Hokkaido showed essentially the same behavior and vertical distribution (Ishida et al. 2001) as seen in the Bering Sea and North Pacific on our tags and those of other Japanese investigators (Wada and Ueno 1999; Azumaya and Ishida 2005). Data from a DST demonstrated a clear diel vertical movement pattern, with the fish within the upper 10 m at night and between the surface and 50 m during the day. When they enter the warmer (16°–20°C) coastal waters near Japan, chum salmon may move to very deep waters during the day. Japanese trawl fisheries in September–December encountered chum salmon at a range of 150–460 m, with most between 200 and 350 m (Ueno 1992, 1994). Fish were almost always captured during daylight hours, with few caught at night. This conforms to data from our data tags and those of Japanese scientists (Wada and Ueno 1999; Azumaya and Ishida 2005), where chum salmon entering coastal waters may spend several days with daytime excursions to several hundred m. These deepest dives were not found in DST studies of chum salmon in coastal waters of the island of Honshu, Japan, by Tanaka et al. (2000, 2001), possibly because the fish were likely past the deep dive phase of their migration, but fish frequently dove to 100–200 m. Deeper diving was most common in October and ceased by December as surface temperatures cooled and the thermocline shifted down. The inference is that fish were conserving energy by avoiding high surface temperatures (Tanaka et al. 2000).

In North America, a coastal trolling study in the Strait of Juan de Fuca demonstrated differences in depth of capture among species (Beacham 1986). Coho were closer to the surface than pinks and sockeye, which were in turn shallower than Chinook. A series of studies using ultrasonic tags tracked sockeye and Chinook salmon and steelhead trout (*O. mykiss*) in British Columbia coastal waters (Quinn 1988; Quinn et al. 1989; Ruggerone et al. 1990; Candy and Quinn 1999). Sockeye were in the upper 30 to 40 m, closer to the surface at night and slower swimming. The mean depth for Chinook was 70 m (usual range 7–200 m), with maximum depths between 300 and 400 m. The fish were generally at shallower depths during the day (25–64 m) than at night (49–78 m). Steelhead spent 72% of their time in the top 1 m, with few movements deeper than 7 m.

In fresh water, juvenile sockeye salmon in lakes are the only species that undertakes major vertical migrations. Patterns of migration vary across lake systems and with the age of fish, but in most populations, juveniles seem to move to the surface at dusk to feed, and are found deeper in the lake for much of the remainder of the day (overview in Quinn 2005). Reasons for vertical migration, including pursuit of prey, avoidance of predators, and thermoregulation, have been reviewed by Quinn (2005) and by Clark and Levy (1988) and Levy (1990), who postulated a framework including all three reasons. Growth (determined by feeding and temperature) was balanced against risk (predation). Immature and maturing salmon at sea are under similar constraints, but their pattern of vertical migration differs. In some lakes, juvenile sockeye descend again after dusk, while at sea, most salmon seem to remain near the surface. Brett (1971) hypothesized that lake surface temperatures may be too warm for the most efficient digestion and growth. Immature and maturing salmon at sea usually do not remain at depth during the day, but frequently return to the surface. It seems unlikely that their frequent and regular daytime vertical movements are due mainly to escape from predators, and descending speeds are slower than ascending speeds (Azumaya and Ishida 2005). Salmon may be descending in pursuit of food, because many of their prey (such as euphausiids, copepods, squid, and myctophids) undergo diurnal vertical migrations. Food is found in salmon stomachs throughout the day, although the occurrence of prey species may vary with time of day (Pearcy et al. 1984; Davis et al. 2000). Salmon may be feeding on prey whose daytime vertical range overlaps with their vertical foraging range. During the day, prey may be easier to see from below silhouetted against the lighter background above. Azumaya and Ishida (2005) concluded that regulation of body temperature was controlled by vertical movements and that maintenance of body temperature for growth and maturation may be a significant reason for the vertical excursions.

Results from data tags are generally in line with previously reported information. However, they illuminate some aspects of behavior, such as changes from relatively ‘flat’ behavior near the surface at night to movements up and down in the water column during daylight hours. This daytime movement shows that salmon do not move down to a fixed depth, but are in frequent vertical motion, meaning an “average” daytime depth, such as obtained from nets or hooks, may not give a full picture of the overall vertical distribution. Also, it does not seem that individual salmon are “stratified” during the day, with some near the surface and some deeper, but most are moving vertically. Data showing nighttime distribution close to the surface confirms that salmon are in very shallow waters, and confirms conjectures of why salmon abundance drops at night in surveys which use gear such as trawls and hydroacoustics which do not fully sample near surface waters (e.g., Nero and Huster 1996 and trawl data in this report). A survey that used surface gillnets (to 6 m) in day and night sets caught more fish at night (Manzer 1964), and commercial and research surface gillnetting by Japanese vessels is intentionally conducted with overnight deployment of surface gillnets because catches are higher (Ueno et al. 1969).

Data tags also allow a fuller picture of vertical distributions, with information on occasional or rare excursions to depths deeper than normal. Many other studies have been limited by depths fished, for example only setting nets to depths of 20 m or 40 m. While not common for sockeye, pink, and coho salmon, occasional movements to greater depths by these species show they are capable of using this part of the habitat. A more detailed analysis of salmon behavior is possible than with coarser sampling gear, such as deep gillnets or trawls with large vertical openings. While knowledge that distribution is within the top 40 or 60 m may be adequate for some purposes, knowledge of movements within that range may also be of use. The data from tags can either clarify or contradict some previous inferences. Manzer (1964) and Beacham (1986) found coho nearer the surface than sockeye and pink, while tag data indicate that sockeye have the shallowest distribution.

Better understanding of how salmon move through the ocean will require data throughout the marine residency. Detection of possible modifications in their vertical distribution due to factors such as competition and changes in ocean conditions will necessitate better baseline data now and continued monitoring in the future.

CONCLUSIONS

In coastal waters, we observed juvenile salmon near the surface, in depths that were usually < 15 m , and within the top 40 m when adults. In offshore waters, salmon are usually within the top 40 to 60 m, above the thermocline, but occasionally are found from 80 to 120 m deep. They usually were near the surface at night, and moved vertically during the day. Chum and Chinook salmon may go much deeper. Sockeye salmon seemed to have the shallowest vertical distribution, followed by pink, coho, chum, and Chinook salmon. There were many exceptions to these generalizations. Vertical movements may change daily, seasonally, or between years.

Limited hydroacoustic data on vertical distributions offshore in winter indicate that salmon were within the top 40 m, similar to depths in summer. Vertical ranges of Chinook salmon in coastal and shelf areas were deeper in summer in the Bering Sea, but deeper in winter off the U.S. West coast. Data from a Chinook in the Bering Sea displayed several different patterns of vertical distribution that changed seasonally.

Because of constant changes in vertical distribution, one must beware of limited term data such as catches of fish or short-term tracking. There is a need for more long-term data, throughout the marine residency of single fish, and for gear that provides a fine enough resolution and complete coverage of salmon depths. Baseline data and monitoring will be needed to detect changes in vertical distributions over multi-year periods.

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