Behavior of adult chinook salmon (*Oncorhynchus tshawytscha*) in British Columbia coastal waters determined from ultrasonic telemetry

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Abstract: To characterize adult chinook salmon (*Oncorhynchus tshawytscha*) migratory behavior, we used ultrasonic tracking to describe their vertical and horizontal movements in upper Johnstone Strait, British Columbia during 1990–1992. Movement patterns varied: several fish showed a postrelease "escape" response and a protracted "recovery" period, with evidence of diel patterns of vertical and horizontal movements becoming apparent after 8 h. After release, 12 of the 32 chinook salmon that were tracked tended to dive deep. Chinook salmon that dived deep (>200 m) were significantly larger than fish that remained nearer the surface (mean fork length, 87.2 vs. 77.3 cm, respectively), and deep diving was not correlated with aspects of handling that might have stressed the fish. The mean depth of travel calculated over all tracks was 70 m and the maximum depths were between 300 and 400 m. Average depths of travel were shallower during the day (25–64 m) than at night (49–78 m). Overall, mean ascent and descent rates were similar (11–12 m/5 min). Gross travel rates (ground speed), defined as the distance moved during 5-min intervals, averaged 1.9 km/h, but tidal currents could have influenced these estimates. Net travel rates, defined as the distance between the point of release and track termination, were slower than gross rates, averaging 0.60 km/h. Average grounds speeds were more rapid during the day (1.9–3.2 km/h) than at night (1.7–2.5 km/h). Compared with sockeye salmon tracked in the same area during 1985–1986, chinook salmon moved more slowly, in both gross and net travel rates, and swam deeper.

Résumé : Dans le but de caractériser le comportement migrateur du Saumon quinnat (*Oncorhynchus tshawytscha*), nous avons utilisé la technique de repérage aux ultrasons pour décrire les déplacements verticaux et horizontaux des poissons dans la partie supérieure du détroit de Johnstone, Colombie-Britannique, de 1990 à 1992. Les déplacements se faisaient selon des patterns variés : plusieurs poissons ont manifesté une réaction de « fuite » consécutive à leur relâchement, suivie d'une courte période de « récupération » et les patterns quotidiens de déplacements verticaux et horizontaux sont devenus apparents au bout de 8 h. Après leur relâchement, 12 des 32 saumons suivis tendaient à plonger en profondeur. Les saumons qui plongeaient en eau profonde (>200 m) étaient significativement plus longs que les poissons qui restaient plus près de la surface (longueur moyenne à la fourche 87,2 vs. 77,3 cm respectivement) et ces plongées en profondeur n'étaient reliées à aucune manipulation qui ait pu stresser les poissons. La profondeur moyenne de tous les déplacements a été estimée à 70 m et les profondeurs maximales atteintes se situaient entre 300 et 400 m. La profondeur moyenne des déplacements était moins grande durant le jour (25–64 m) que durant la nuit (49–78 m). Dans l'ensemble, la vitesse des montées et des descentes était la même (11–12 m/5 min). La vitesse brute de déplacement (vitesse de base), définie comme la distance parcourue au cours d'un intervalle de 5 min, était en moyenne de 1,9 km/h, mais les courants de marée peuvent avoir influencé les estimations. La vitesse nette de croisière, définie comme la vitesse parcourue entre le point de relâchement et la fin du trajet, était inférieure à la vitesse brute, de 0,60 km/h en moyenne. Les vitesses de base moyennes étaient plus rapides durant le jour (1,9–3,2 km/h) qu'à la nuit (1,7–2,5 km/h). Comparativement à des Saumons rouges suivis dans la même zone en 1985–86, les Saumons quinnats se déplacent plus lentement (aussi bien la vitesse de déplacement brute que la vitesse nette) et nagent à une profondeur plus grande.

[Traduit par la Rédaction]

Introduction

The oceanic distribution patterns and homing migrations of adult Pacific salmon (*Oncorhynchus* spp.) have been studied for decades (e.g., reviews by Neave 1964; Royce et al. 1968; Groot and Margolis 1991). Much of the empirical in-formation has been collected on the most numerous species of salmon (pink, *Oncorhynchus gorbuscha*; sockeye, *Oncorhynchus nerka;* and chum, *Oncorhynchus keta*). These species feed primarily or exclusively in the pelagic regions of the Gulf of Alaska, the Bering Sea, and the North Pacific Ocean, and maturing adults migrate relatively rapidly to-

wards the coast from the open ocean and through coastal waters towards their natal stream (French et al. 1976; Neave et al. 1976; Takagi et al. 1981). In contrast, coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon are often found in coastal waters (though they also occur offshore), and their homeward migrations may be slower than those of other species (Godfrey et al. 1975; Major et al. 1978; Fisher and Pearcy 1987); in addition, their migration patterns are less well known.

Ultrasonic telemetry has provided detailed information on the migratory behavior of individual salmon in the open ocean (coho: Ogura and Ishida 1992; sockeye, chum, pink, and chinook: Ogura and Ishida 1995) and in coastal waters (sockeye: Madison et al. 1972; Stasko et al. 1976; Quinn 1988; Quinn et al. 1989; pink: Stasko et al. 1973; steelhead trout: Ruggerone et al. 1990). These studies indicate that sockeye, chum, and pink salmon and steelhead trout tend to swim near their most efficient (i.e., least cost) speed of about 1 body length/s, but that coho and chinook salmon swim more slowly. Despite the evidence that migration patterns differ among salmon species, most information has been obtained for the numerous species and large stock complexes, and inferences about salmon migrations are often based on such data. In particular, Fraser River sockeye salmon have been the focus of intensive study, including tagging (e.g., Verhoeven and Davidoff 1962), analysis of catch records (Groot and Quinn 1987), tracking (Madison et al. 1972; Stasko et al. 1976; Quinn et al. 1989), and modeling (Pascual and Quinn 1991; Thomson et al. 1992, 1994; Dat et al. 1995).

Chinook salmon are the least abundant semelparous species of salmon (Groot and Margolis 1991) and many populations are in jeopardy (Nehlsen et al. 1991; Washington Department of Wildlife and Western Washington Treaty Indian Tribes 1993; Slaney et al. 1996). Their tendency to mature at a greater age than other species (Groot and Margolis 1991) and the coastal distributions and relatively slow homeward migrations of many populations make them particularly vulnerable to overfishing and greatly complicate their management (Walters and Riddell 1986). They are sought by commercial and recreational fisheries and may be taken as by-catch in fisheries directed at other salmon species, such as the sockeye salmon fisheries in Johnstone Strait, British Columbia. In addition, their tendency to swim deep (Ogura and Ishida 1995; Orsi and Wertheimer 1995) can result in their being intercepted by trawlers fishing for demersal and benthic fishes (Myers and Rogers 1988; Erickson and Pikitch 1994). Their capture in directed fisheries and as by-catch depends on such basic behavioral patterns as depth of travel, proximity to shore, travel rate, and diel activity rhythms, but such patterns are not well-documented. Therefore, our purpose was to characterize chinook salmon movements in Johnstone Strait, B.C., using ultrasonic telemetry. Our primary objectives were to determine their depth distribution (average depth and rates of decent and ascent), rates of horizontal travel, proximity to shore, and diel changes in depth and speed. The secondary objective was to compare the information on chinook salmon with data collected in this area on sockeye salmon in 1985 and 1986 (Quinn and terHart 1987; Quinn 1988; Quinn et al. 1989). This comparison will highlight differences in the behavior of these species and may facilitate management of the mixed-species fishery in the area (Candy et al. 1996).

## Materials and methods

Data collection

Chinook salmon were captured by commercial seine vessels and tracked in upper Johnstone Strait in the summers of 1990, 1991, and 1992. Johnstone Strait is a relatively deep (>300–400 m in many areas) weakly stratified body of water with mixed semidiurnal tides and strong tidal currents (Thomson 1976, 1977, 1981). Several aspects of the capture process were recorded to test possible effects on the subsequent behavior of the fish (see Candy et al. 1995 for details of the methods). Fish were caught by two types of landing procedures: "stern," in which the chinook salmon was taken from the deck after the catch had been pulled over the stern of the vessel; and "side," in which the fish was dip-netted from the seine net while it was held alongside the vessel. Landing time was the period from the commencement of net retrieval to the moment when the chinook salmon was dip-netted from the pursed net or landed on the deck of the vessel. Tagging time was the period after the fish was landed and before it was released. The chinook salmon were measured (fork length) and assessed for capture-induced injury (Candy et al. 1995). Each fish had a pressure sensitive ultrasonic transmitter (74 × 16 mm, 13 g; Vemco Ltd., Shad Bay, N.S.) inserted into its stomach, and also received a numbered spaghetti tag (Floy Tag Co., Seattle, Wash.) for external identification. Except for the potential of tag regurgitation, insertion of the transmitter into the stomach appears to be the best method of tag attachment, as this method has a minimum effect on swimming performance and behavior (Mellas and Haynes 1985).

We used several different tracking and tagging vessels during the study (Candy et al. 1995) but, in all cases, fish were released near the capture site and followed at a maximum range of 400–500 m with a directional hydrophone and receiver–decoder (Vemco Ltd.). The transmitter produced a signal on a fixed frequency from 50 to 76.8 kHz, with a pulse interval proportional to pressure (i.e., depth). The transmitters were calibrated to ±1 m for transmitters with a 0- to 100-m depth range (used in 1990) and to ±2 m for transmitters with 0- to 200-m depth range (used in 1991 and 1992). Fish depths (recorded to the nearest metre) and vessel position (determined by locally corrected Loran C readings and, in 1992, a GPS (global positioning system)) were recorded at 5-min intervals. Our goal was to track fish for a minimum of 24 h, but some tracks were suspended, owing to signal loss, inclement weather, shallow water, or difficulty in maneuvering through the gill-net fishery at night. Similar methods of capture, tagging, and release were used for sockeye salmon tracked in 1985 and 1986 (Quinn et al. 1989).

Data analysis

Our initial analytical approach was to plot the data on depth of travel over time. Inspection revealed a great range of depths and an apparent decrease in depth over the duration of the tracks. In many cases there was a particularly deep dive within a few hours of release, and we considered the possibility that this represented postrelease "escape" behavior. Based on maximum dive depth, chinook salmon were divided into two categories thought to represent a behavioral response to the capture and release: salmon that dived >200 m deep and salmon whose maximum dive depth was <200 m. Examination of the data indicated that many of the chinook salmon displayed exaggerated dive behavior shortly after release that was not shown later. Therefore, the first 8 h of the tracks were not analyzed for diel movement, under the assumption that the fish were undergoing a period of postrelease recovery. Swimming depths recorded at 5-min intervals were used to calculate mean depths and rates of ascent and descent (depth change over 5-min intervals).

Fig. 1. Cumulative (1990–1992) depth distribution of all chinook salmon combined; bars represent the proportion of time spent at 20 m depth intervals. An example of oceanographic conditions in Johnstone Strait is also shown: the temperature (solid) and salinity (dotted) profiles in Upper Johnstone Strait, 4 July 1990.
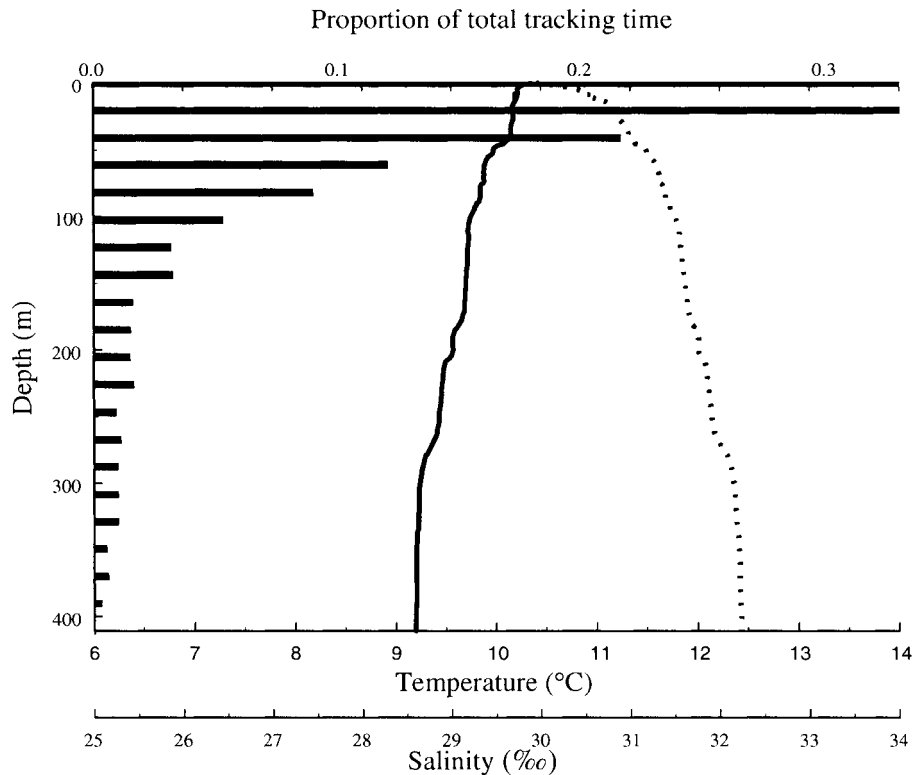
Three aspects of horizontal movements were analyzed: gross movement, net movement, and distance from shore. Gross movement was the sum of the distances moved during 5-min intervals, and ground speed was the gross distance divided by the track's duration. Gross movement is the result of two vectors: the speed and direction of the currents and the active swimming of the salmon. Net distance was the distance between the point of release and the point of track termination, and net travel rate was the net distance per hour. Distance to mean low water mark on the nearest shoreline was measured from 1 : 20 000 scale electronic charts for both chinook- and sockeye-salmon tracks at 0.5-h intervals, using the graphics plotting program Seaplot®.

For analysis of the relationships between fish size and the possible stress associated with capture and subsequent behavior, continuous data were divided into the following classes: fish size (small, <70 cm; medium, 70–85 cm; or large, >85 cm), landing time (short, <15 min; medium, 15–30 min; or long, >30 min), and catch size (small, <200 fish; medium, 200–500 fish; or large, >500 fish). The interactions of maximum dive depth with tagging time, landing time, landing procedure, fish size, and catch size were tested with the log likelihood ratio or G test (Sokal and Rohlf 1981).

Results

Tracking operations

All tagged fish were captured in sets with one end of the net secured to land on the Vancouver Island side of upper Johnstone Strait (inset in Fig. 3). Mean fork lengths of the chinook salmon we tracked were similar to those sampled during the 1987–1990 commercial sockeye salmon seine fishery in upper Johnstone Strait (80.1 and 78.9 cm, respectively), but we tracked more chinook salmon of intermediate size (80–90 cm) than had been sampled in the fishery (Nagtegaal et al. 1990, 1993a, 1993b; Nagtegaal and Riddell 1994). We tracked 49 chinook salmon but analyzed data from only 32 fish, because the other tracks were short or we suspected that the fish had died (Candy et al. 1996). Fish used in the present analysis were tracked for between 7 h 55 min and 32 h 42 min (mean, 19 h 26 min), with 13 being tracked for more than 24 h. Most (72%) were released for tracking in the morning between 05:00 and 12:00.

Vertical movements

The average depth of travel of the 32 fish was 70 m (SD = 57 m) and the maximum depth recorded was 398 m. Johnstone Strait was characterized by relatively cool saline waters with weak surface stratification (Fig. 1). Individual chinook salmon showed a range of vertical distributions and movement patterns, complicating the analysis of the depth data. Based on inspection of the maximum dive depths, fish were divided into two classes. Twenty fish remained <200 m deep and 12 fish exceeded a 200-m depth during at least part of the track. These dive patterns were not associated with handling procedures. Specifically, deep-diving and shallow-diving fish did not differ in landing time (mean, 19.9 vs. 20.0 min, $G = 0.31$, df = 2, $P > 0.05$), tagging time (mean, 14.3 vs. 12.0 min, $G = 1.05$, df = 2, $P > 0.05$), number of salmon caught in the net with them ($G = 0.56$, df = 2, $P > 0.05$), nor the type of landing operation ($G = 0.58$, df = 2, $P > 0.05$). However, deep-diving fish were larger than shallow-diving fish (mean, 87.2 vs. 77.3 cm, $G = 8.06$, df = 2, $P < 0.05$).

Fig. 2. Summary of average hourly horizontal and vertical movements and standard error of the mean for chinook salmon tracked in upper Johnstone Strait. Mean depth (A and E), vertical velocity (V. vel.) (B and F), horizontal velocity (H. vel.) (C and G), and distance to shore (Shore dis.) (D and H) by tracking interval and time of day. The time of day graphs (E, F, G, and H) exclude the first 8 h of the track.
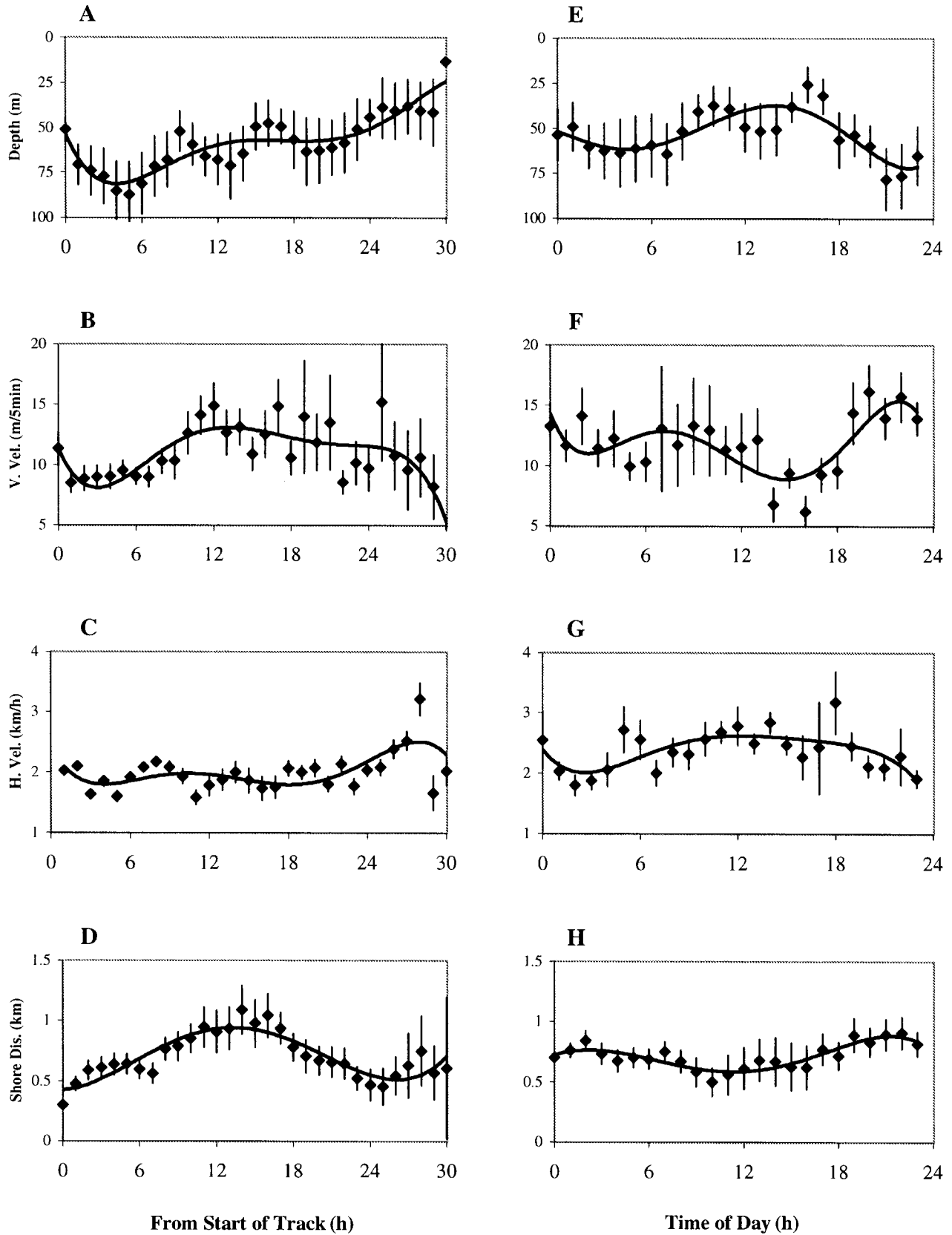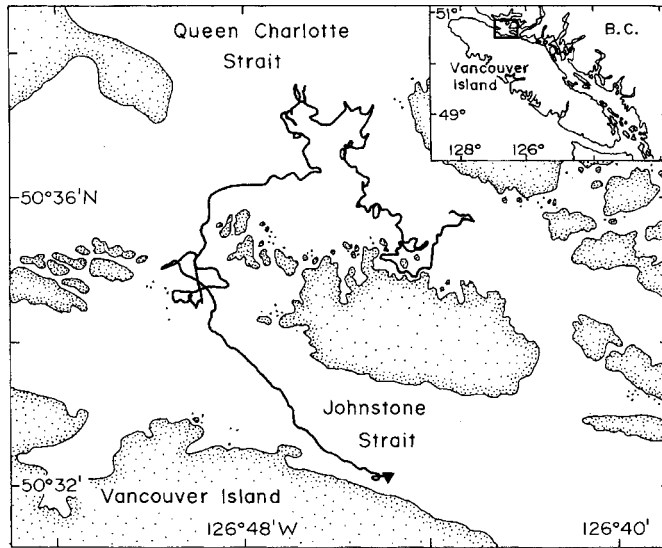

From Start of Track (h)

Time of Day (h)

Fig. 3. Horizontal movements of chinook salmon No. 9116 that was released 21 August 1991 and tracked in upper Johnstone Strait for 34 h 45 min. The triangle marks the release site.

Fig. 4. Horizontal movements of chinook salmon No. 9111 that was released 15 August 1991 and tracked in upper Johnstone Strait for 28 h 35 min. The triangle marks the release site.

those fish that moved northwards from the narrow Johnstone Strait and into the wider Queen Charlotte Strait. However, there was considerable variation in behavior among fish. Some moved along the shoreline (e.g., Fig. 4), whereas others moved with tidal currents and milled around in areas of mixing water (e.g., Fig. 3).

Eight of the 49 fish (16%) were recovered in fisheries or on spawning grounds 6–62 days after tracking was terminated. Four were recovered at hatcheries in the Strait of Georgia (two at Big Qualicum and one each at Quinsam and Nanaimo), one each from sport fishers in the Strait of Georgia and the west coast of Vancouver Island, and one each from commercial fishers in Johnstone Strait and the Strait of Juan de Fuca. The estimated minimum distances traveled ranged from 22 to 500 km, or 3–30 km/day net travel. Fish recovered from hatcheries had a lower daily travel rate; perhaps they were in the hatchery for some time before they were discovered. The average travel rate for the four fish not recovered in hatcheries was 15.2 km/day.

Diel activity patterns

Diel changes in behavior were analyzed 8 h after the start of tracking, to avoid the possible confounding effects of handling on behavior. Of all the characteristics measured, variation in depth showed the strongest evidence of a diel movement pattern. Chinook salmon tended to swim closer to the surface during the day (Fig. 2E); means ranged from 49–78 m at night (19:00–04:00) to 25–64 m during the day (05:00–18:00) (t test, $P < 0.05$). Compared with their behavior during the night, in the daytime, the fish showed lower rates of vertical movement (Fig. 2F), tended to travel slightly closer to shore (Fig. 2H), and traveled at higher horizontal velocities (Fig. 2G). Mean speeds ranged from 1.7–2.5 km/h during the night (19:00–04:00) to 1.9–3.2 km/h during the day (05:00–18:00) (t test, $P < 0.05$).

Release and recovery behavior

Analysis of average ground speeds, dive depths, ascent and descent rates, and distances to shore indicated a pattern of chinook salmon behavior after release. Some fish dived deeply (or sank passively) after release before ascending 5–
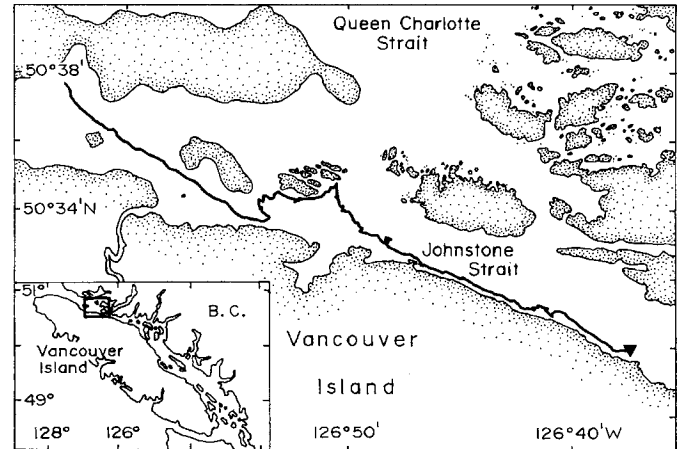
Within 6 h of release, over 50% of the deep-diving fish had attained their maximum track depth, whereas only 25% of the shallow-diving fish had attained their maximum track depth. Deep-diving fish tended to move back towards the surface about 5–8 h after they were released, and their average depth of travel continued to decrease up to 30 h after the start of tracking (Fig. 2A). The mean ascent and descent rates for all the chinook salmon combined were similar (11.8 vs. 11.5 m/5 min; t test, $P > 0.05$). However, the rates of ascent and descent varied among fish (ANOVA, $P < 0.001$). Deep-diving (larger) fish had greater ascent and descent rates than shallow-diving fish (mean ascent = 15 m/5 min vs. 10 m/5 min; t test, $P < 0.05$; mean descent = 14 m/5 min vs. 10 m/5 min; t test, $P < 0.001$). Overall, average rates of vertical movement peaked 8–24 h after release, then decreased as the fish moved nearer the surface (Fig. 2B).

Horizontal movements

Average ground speeds ranged from 0.7 to 2.7 km/h for individuals (mean of all fish: 1.9 km/h, SD = 0.4 km/h). There was significant variation in ground speed among fish (ANOVA, $P < 0.001$), but ground speeds of deep-diving and shallow-diving fish did not differ (t test, $P > 0.05$), nor did those of large (>80 cm) and small (≤ 80 cm) fish (t test, $P > 0.05$). The ground speeds corresponded to an average of 0.7 body lengths/s (range = 0.2–1.0 body lengths/s). There was no correlation between ground speed and depth of travel using average depths and speeds of individuals or for average depths and speeds on an hourly basis. Average horizontal velocities were constant over the duration of tracking (Fig. 2C). Net travel rates were considerably slower than ground speeds (average of all fish, 0.60 vs. 1.9 km/h), reflecting the circuitous paths of 22 fish (e.g., Fig. 3), but the movements of 10 fish were very directional (e.g., Fig. 4).

Average distance to shore was 0.7 km and ranged from 0.2 to 1.7 km. Overall, fish tended to move offshore from the release site and then start moving back towards shore about 15 h after release (Fig. 2D). Distance to shore increased for

Table 1. Mean and range for horizontal and vertical movement of sockeye and chinook salmon tracked in Johnstone Strait.

	No. of fish	Ground speed (km/h) Mean	Range	Ground speed (body length/s) Mean	Range	Net speed (km/h) Mean	Range	Swimming depth (m) Mean	Range	Ascent rate (m/5 min) Mean	Range	Descent rate (m/5 min) Mean	Range	Orientation factor (net/gross distance) Mean	Range	Minimum distance to shore (km) Mean	Range
Chinook	32	1.9	0.7–2.7	0.7	0.2–1.0	0.60	0.04–1.3	69.9	7.1–200.8	12	1–115	12	1–112	0.31	0.03–0.71	0.7	0.10–1.7
Sockeye	16	2.2	1.3–3.7	0.9*	0.5–1.75	0.88	0.18–3.0	14.9	6.0–38.5	8	1–45	7	1–39	0.37	0.03–0.85	1.1	0.4–3.4

*Data not available for all fish.

6 h later (Fig. 2A). At release, fish tended to move offshore (Fig. 2D), travelling at lower or near average horizontal and vertical velocities (Fig. 2C). Lower than average vertical velocities immediately after release suggest that the fish may be going through a period of reduced activity (Fig. 2B). Fish that deep dive are probably passively sinking rather than actively swimming downward.

Comparison with sockeye salmon data

We analyzed data from 16 sockeye salmon tracked in Johnstone Strait and nearby waters (Queen Charlotte Strait and Discovery Passage) in 1985 and 1986 (Quinn et al. 1989). Overall, the sockeye salmon traveled much closer to the surface than the chinook salmon (means: sockeye = 14.9 ± 7.5 (SD) m, chinook = 69.9 ± 57.3 (SD) m; t test, $P < 0.001$) and ascended and descended at about half the rate of the chinook salmon (mean ascent rate = 8 m/5 min; t test, $P < 0.001$; mean descent rate = 7 m/5 min; t test, $P < 0.001$; Table 1). The sockeye salmon also maintained a nearly constant depth more often than the chinook salmon (0–5 m/5 min; Fig. 5). Sockeye salmon ground speeds were faster than those of chinook salmon (2.2 vs. 1.9 km/h, respectively; t test $P < 0.05$), especially when expressed as body lengths per second (0.9 vs. 0.7 lengths/s for sockeye and chinook salmon, respectively; t test, $P < 0.05$). Chinook salmon traveled closer to shore (average minimum distances were 0.7 and 1.1 km for sockeye and chinook salmon, respectively; t test, $P < 0.05$). However, this was confounded by the fact that the chinook salmon were caught and released closer to the shore (average 0.3 vs. 1.5 km for sockeye and chinook salmon, respectively; t test, $P < 0.001$). The average orientation factor (ratio of net to gross travel rates) was slightly lower for the chinook salmon (0.37 vs. 0.31 for sockeye and chinook salmon, respectively; t test, $P > 0.05$).

Discussion

We used ultrasonic telemetry to characterize the horizontal and vertical movements of chinook salmon, and the hypothesized species-specific patterns were observed. Chinook salmon swam deeper and traveled slower than sockeye salmon. Tidal currents in Johnstone Strait are complex, varying horizontally and vertically, and often exceed 20 cm/s (Thomson 1976, 1977, 1981; Quinn 1988), hence swimming is difficult to distinguish from horizontal advection by currents. Like chinook salmon tracked in the Columbia River estuary (Olson and Quinn 1993), the fish tended to move with the tidal currents and milled during periods of low current velocity, but the difficulty in determining how much of the fish's displacement resulted from its own swimming complicates the interpretation of the data.

The travel rates of chinook salmon in Johnstone Strait were slower than those of sockeye salmon in the same area despite their greater size, and the chinook salmon also had a lower ratio of net to gross travel, indicating that their swimming was less directional. Maturing chinook salmon may travel at a slower rate than sockeye salmon, which migrate rapidly through Johnstone Strait towards the Fraser River (Verhoeven and Davidoff 1962). Average rates of travel for chinook salmon bound for spawning rivers ranged from 11.5 to 25.1 km/d (Healey and Groot 1987), which is consistent

Fig. 5. Frequency of depth change by 5-min intervals recorded for chinook salmon (left-diagonal bars) in the years 1990–1992 and for sockeye salmon in the years 1985–1986 (right-diagonal bars) in upper Johnstone Strait.
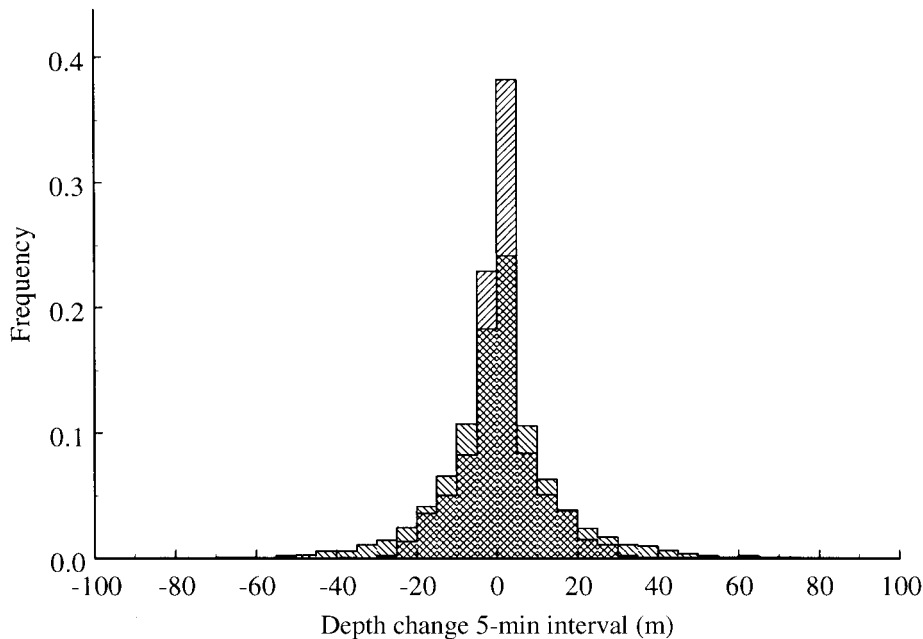
with the 0.7–2.7 km/h determined by this study. In addition, based on the eight tag recoveries, most of the chinook salmon moved southwards, but they were likely migrating to a wider range of locations and on a wider range of schedules than the sockeye salmon. Finally, the chinook salmon may not all have been maturing when we caught them, hence, not migrating homeward. Maturing and immature chinook salmon originating from a wide range of locations forage and migrate through the waters between Vancouver Island and the mainland of British Columbia, whereas virtually all sockeye salmon are maturing individuals migrating towards the Fraser River. The immature chinook salmon would not be expected to travel in as directed a manner as maturing ones. Thus the lower rate of movement and smaller ratio of net to gross travel by chinook salmon do not necessarily indicate poorer orientation than sockeye salmon.

Salmon are thought to use a wide range of orientation mechanisms to migrate from feeding areas at sea to their natal streams (Harden Jones 1968; Dittman and Quinn 1996). The closer proximity to the surface and greater horizontal velocities observed during the day suggest that the salmon use visual clues, such as the sun's position or light-polarization patterns, for orientation (Dittman and Quinn 1996). At night, more exaggerated vertical movements and reduced horizontal movement suggest that other stimuli, such as salinity, temperature, and olfaction, may become the dominant means of orientation, because visual clues are unavailable. Depths of travel vary with oceanographic conditions, as shown by the fact that sockeye salmon in the Strait of Georgia spent much less time near the surface than they did in Johnstone Strait (Quinn et al. 1989).

The data revealed much greater maximum and average depths of movement under similar oceanographic conditions for chinook salmon than for sockeye salmon in this region (Quinn et al. 1989), or for steelhead trout in a coastal mainland British Columbia inlet (Ruggerone et al. 1990), and

were consistent with the travel depth of chinook salmon in the central Bering Sea (Ogura and Ishida 1995). These results were also consistent with the greater tendency for chinook salmon to be taken as by-catch in trawl fisheries directed at groundfish species (e.g., Myers and Rogers 1988; Erickson and Pikitch 1994). Erickson and Pikitch (1994) reported that chinook salmon were taken in bottom trawls at depths of from 100 to 482 m (primarily between 100 and 400 m) during the winter, but were taken less frequently in shallower water (<220 m) in the summer off the U.S. west coast.

It is not clear whether the depth of travel is an adaptation to foraging or to predator avoidance. Small fishes on which chinook salmon feed are abundant in the near-surface waters, and visual foraging would presumably be difficult at the depths where the chinook salmon swim, although they may have adaptations for foraging at low light levels. Their large size would seem to make chinook salmon less vulnerable to predation than other salmon species, so one might expect them to travel near the surface. However, Johnstone Strait has a large community of piscivorous killer whales (*Orcinus orca*) in the summer, and their preferred prey are chinook salmon (Ford et al. 1998). The extent to which depth of travel and vertical movements reflect orientation mechanisms, physiological preferences, or other behavior patterns, such as foraging and predator avoidance, remains to be determined.

In addition to the generally deep distribution, the chinook salmon showed an initial dive immediately after release, which is similar to other salmon species (Quinn et al. 1989; Ruggerone et al. 1990; Ogura and Ishida 1992, 1995). This could be either an escape response or a response to severe stress. There was no correlation between deep diving in chinook salmon and any aspect of handling (i.e., landing time, tagging time, catch size, or landing procedure). This, combined with the fact that larger fish dived deeper than smaller

fish, indicated that deep diving may represent an escape response that is more characteristic of larger salmon. Perhaps individuals who have completed more of their growth are more risk averse in their foraging than smaller individuals (Holtby and Healey 1990). When the initial dive occurred, rates of vertical movement and possibly horizontal movement were reduced. The combined pattern of deep diving, reduced travel rates, and movement offshore occurred in many chinook salmon and characterized a postrelease response. Analysis of vertical and horizontal movement indicated that most chinook salmon returned to "normal" (or at least consistent) behavior sometime after 6–8 h of tracking but, in some cases, were still moving onshore 24 h later. Given the high cost of tracking salmon for several days and the uncertainty as to when the fish begin displaying representative behavior, future studies might employ miniature depth-sensitive data loggers rather than transmitters. Had we done so, data would have been obtained for only eight fish and no information would have been obtained on horizontal movements. However, the extended data (6–62 days) might have been more reliable and the money saved could have been used to purchase more tags.

Acknowledgements

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