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Behavior of chum salmon as revealed by micro data loggers off the Sanriku coast, Japan: A review

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The homing season of chum salmon in the Sanriku coastal area is generally late September to January. The surface water temperature is 20°C at the beginning of the season and decreases to 12°C at the end. This temperature condition is very tough for the homing migration of chum salmon, since they are typical cold-water species. How do they behave in the waters where temperatures can be close to their upper lethal limit? We monitored swimming behavior of salmon using micro data-loggers to study the relationship between homing behavior and ambient temperature. Seasonal changes in seawater temperature transformed the salmon behavior from deep diving to surface swimming. The deep diving is a type of behavioral thermoregulation in thermally stratified water with high surface temperature, whereas surface swimming helps the salmon to locate their natal rivers. Sexual maturation induced the salmon to seek their natal river in the surface water, even if their temperature was high. An analysis of the vertical movements of the salmon indicated that salmon are negatively buoyant throughout the dive, and thus, the energy cost for deep diving cannot be negligible. Our data indicate the high behavioral adaptability of salmon to such thermally stratified water with high surface temperature.

Key words: chum salmon, migration, vertical movement, swimming speed, data logger

INTRODUCTION

Chum salmon is the most abundant and commercially important salmonid fish in Japan. Like other Pacific salmon, chum salmon have an anadromous life history. Their spawning season is autumn to early winter in Japan. Under natural conditions, eggs are deposited in the gravel of rivers. Hatched alevins stay in the gravel for about a month and, after yolk-sac absorption, the fry swim up from the gravel. In early spring, the fry start a down-stream migration and swim into the sea. They stay for a short period in the bay, and juveniles then start a northward migration to the northern North Pacific Ocean. They usually stay there for two to four years, after which maturing adults start a southward migration to their natal rivers to spawn. In Japan, salmon stocks are under human control. Almost all the homing adults that reach their natal rivers are caught before spawning, eggs are artificially fertilized, and alevins are raised in the hatcheries. Hatchery-raised fry are then released into the river. The released fry continue their migration to the sea, grow in the northern North Pacific Ocean and maturing adults return to their natal rivers like the wild stock. Homing adults are important for Japanese fisheries; they are caught by stationary trap-nets, long lines or gill nets in coastal waters. At present, more than 190 thousand tons of chum salmon are caught per year.

Chum salmon is a typical cold-water fish like other salmonids. Its upper lethal temperature is about 24°C, and the limiting temperature that defines the southern boundary of their Pacific distribution is 10.2°C (Schmidt-Nielsen 1990, Welch et al. 1995). The natural spawning areas of chum salmon are the coasts of the northern North Pacific Ocean, Bering Sea and Sea of Okhotsk. Honshu Island in Japan is the southernmost spawning ground of chum salmon (Kaeriyama 1989). The Sanriku coastal area is one of the southernmost natural spawning places. The homing season of chum salmon in the area is generally late September to January. The surface water temperature is 20°C at the beginning of the season and decreases to approximately 12°C at the end. The high temperature at the beginning of the season is caused by two warm currents that flow off the Sanriku coast, the Tsugaru Warm Current and the Kuroshio. Several warm water masses, originating from the Kuroshio are usually distributed near the Sanriku coast. This temperature condition seems to be physiologically tough for the homing migration of chum salmon. How do salmon behave in such waters where temperatures can be close to their upper lethal limit? This is of interest not only with respect to the biology of chum salmon, but it is also important for understanding the effects of global warming on salmon stocks in the future. Global warming, largely due to the greenhouse effect of carbon dioxide, may have a great impact on the salmon's life history through its effects on seawater temperature. Detailed studies on salmon behavior in the warm water observed off the Sanriku coast may give us an insight on how salmon adapt to global warming. Therefore, we have examined the swimming behavior and ambient temperatures of homing chum salmon off the Sanriku coast.

To study salmon behavior, we used a newly developed micro data logger. Until the late 1990s, salmon behavior was mainly investigated with acoustic transmitters, and several important findings were obtained. For example, homing individuals generally show a preference for shallow water, and vertically stratified hydrostatic features are reported to guide their swimming depth (Døving et al. 1985, Quinn et al. 1989, Ruggerone et al. 1990). When acoustic transmitters are used, researchers must follow the salmon because the transmitters have a limited range of transmission. Thus, the difficulties in tracking have limited such studies to semi-closed systems. The duration of the studies is also limited to a few days or less, and the number of observations was relatively small. Compared with telemetry tracking methods, recovery-type data logger tagging makes it possible to study the swimming behavior of free-ranging salmon in open systems with much less labor, although the position of the salmon is impossible to obtain. An advantage to using chum salmon in such studies is that there is a very high recovery of homing salmon by the fishing industry in Japanese coastal areas. We have conducted data logger-tagging studies since 1995. Starting in 1999, the study has been conducted under the "Cooperative International Research Project on Marine and Coastal Environment", implemented by the Iwate Prefectural Government, Ocean Research Institute of the University of Tokyo, and United Nations University. In the present paper, we will review the results obtained in the study. The detailed data have been published elsewhere (Tanaka et al. 1998, 2000, 2001).

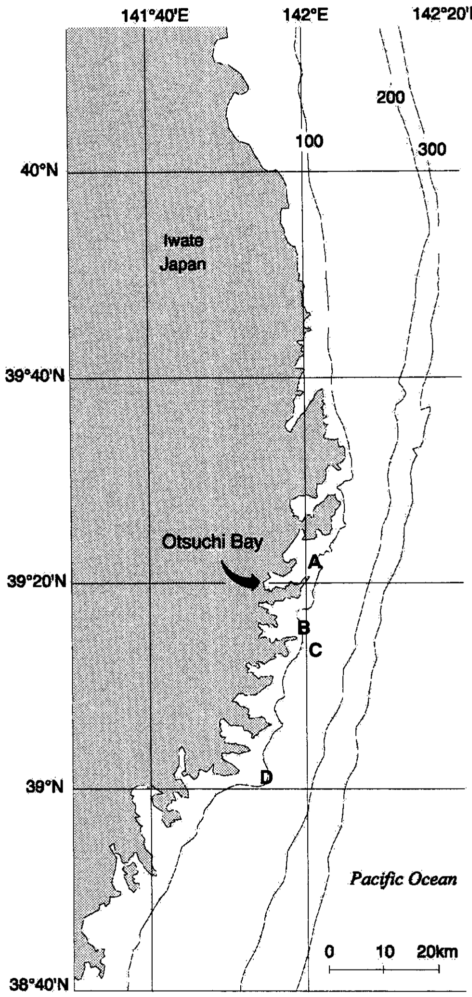

Fig. 1. Map showing the study site off the Sanriku coast, Japan. A to D show the points where tagged salmon were released. Lines indicate 100, 200 and 300 m contours. Modified from figure 1 in Tanaka et al. (2000), the *Journal of Experimental Biology*, **203**, pp. 1825–1833.

METHODS

The behavior of homing adult chum salmon, *Oncorhynchus keta*, was studied off the Sanriku coast, northern Honshu Island, Japan (Fig. 1). We conducted the study in the fall during the homing migration over a period of several years: early December 1995, early October 1996, late October to early November 1996, December 1996, and early October in the years 1997, 1999 and 2001. The study area has a rich stock of chum salmon, which originate from ca. 30 salmon hatcheries. The homing adults that reach the study area are expected to ascend their natal rivers within a few weeks. They usually have empty and contracted stomachs, indicating that they have already stopped feeding in the study area. Chum salmon show a drastic change in their body color during the course of their final maturation. When they first reach the study area, they are at the final stage of vitellogenesis, but have not ovulated yet. At this stage, the fish have a silver body. After several weeks, they reach final maturation and ovulate. Their body color changes from silver to dark yellow-brown, with a typical red color in the belly, which is a second sexual character of chum salmon. Therefore, the body color is a good indicator of their maturational stage. Unless otherwise noted, the salmon used in this study were silver salmon that were expected to be several weeks from spawning.

Experiments in October and November were carried out in Otsuchi Bay. Three rivers, the Otsuchi, Kozuchi and Unosumai Rivers, flow into the Bay. The distance from the river mouths to the mouth of the bay are each about 6.5 km. The mouth of the bay is about 3.5 km wide, and about 90 m deep. Generally, fish were caught with trap nets set at the mouth of Otsuchi Bay, and transferred to the Otsuchi Marine Research Center (OMRC), Ocean Research Institute, the University of Tokyo, which is located at the north coast of Otsuchi Bay. Fish were lightly anesthetized with 2-phenoxy ethanol, and total length and body weight were measured. A data logger was sutured to the left side of the body, below the front edge of the dorsal fin, using nylon ties. The laboratory address and a request to return the data logger were printed on each data logger. Fish were then transferred to a tank with continuous flow of seawater and allowed to recover from the surgery for 2–12 h. After the recovery, fish were transferred to the bay mouth (point A in Fig. 1) and released. The fork length of the salmon used in the study was 55.0–70.5 cm.

Generally in December, salmon caught with trap nets at the mouth of the Otsuchi Bay had already reached their final maturation stage and had a dark yellow-brown body color. They were presumed to be only a few days away from ascending their natal rivers (Hirano et al. 1990). Therefore, in the experiments in December, chum salmon fished by a long line outside the bay (points B, C and D in Fig. 1) were used. On the vessel, data loggers were attached to the fish as described above, and fish were released after about a 60-min recovery. The fork length of the salmon used in the study was 59.0–77.5 cm.

In order to compare the behavior of fully matured fish with that of maturing silver fish, fully matured fish were caught at the mouth of Kozuchi River and transported to OMRC in early October 1996. They were fitted with the data loggers as described above and released at the mouth of Otsuchi Bay (point A in Fig. 1). Moreover, in October 2001, maturing fish with a slight yellow-brown body color were caught at the mouth of Otsuchi Bay, fitted with the data loggers as described above, and released at point A in Fig. 1. These fish were slightly more mature than silver fish, but they still hadn't reached the ovulation stage. The fork length of the salmon used in the study was 52.0–68.5 cm. This experiment was conducted to further examine the effects of maturational condition on the behavior of salmon.

Several types of data loggers (Little Leonard Co. Ltd., Tokyo, Japan) that could record depth and temperature simultaneously were used in our study. They were each cylindrical in shape with diameters of 19–21 mm, lengths of 62–117 mm, and weights of 30–60 g in air and 9–22 g in water. Each was equipped with a flash memory having between 0.5 and 128 megabytes of memory. The depth channel had a maximum range of 200 m, with a resolution of 0.05 m and an accuracy of $\pm$0.5 m. The resolution and accuracy of the temperature channel were 0.02 and $\pm$0.1°C. The interval between sampling times, which was programmed for each salmon, varied from one to five seconds in the depth channel and from five to 15 seconds in the temperature channel. Some of the data loggers were also equipped with speed and acceleration monitors. The speed sensor consisted of a propeller rotation counter. The stall speed of the recorder was 0.3 m/sec. Speeds below this value were indistinguishable from zero. The propeller speed (revolution/sec) was converted to the flow speed using a conversion formula obtained by the preliminary experiments. The acceleration logger was equipped with two piezo-resistive accelerometers along with speed, depth and temperature sensors. The measuring range of the accelerometer was -4 to 4 g (g=9.8 m/sec^2). The data logger was attached to the salmon to record acceleration in two directions: the surging acceleration along the longitudinal body axis of the fish and the swaying acceleration transversely across the salmon's body from right to left. The body angle of the salmon can be obtained from the surging acceleration, whereas the tail beat frequency and amplitude of the tail thrust were detected from the swaying acceleration. Explanations of how these quantities can be obtained from the acceleration data are given in Tanaka et al. (2001).

SEASONAL CHANGE IN SALMON BEHAVIOR

Figure 2 shows a typical pattern of swimming depth and ambient temperature for salmon in October. This is a part of the record of a single fish, number 9706. This individual is a male, but there was no obvious sexual difference in the recorded behavior. Salmon dived to over 100 m and stayed in the deep water for hours. Some individuals recorded depths of more than 200 m. The depth at the point where the data-logger-tagged salmon were released (point A in Fig. 1) was less than 100 m. The present depth data clearly showed that the data-logger-tagged salmon migrated outward from the bay, away from the coastline. The record also showed that salmon repeatedly came back to the surface. In October, the seawater is thermally stratified, and thus, salmon experienced a variation of nearly 10°C in their ambient temperature.

In contrast to salmon in October, salmon in December never made long, deep dives. Figure 3 shows the typical swimming pattern of salmon in December. This record was also obtained from a male, but again there was no obvious sexual difference in their behavior. In December, salmon

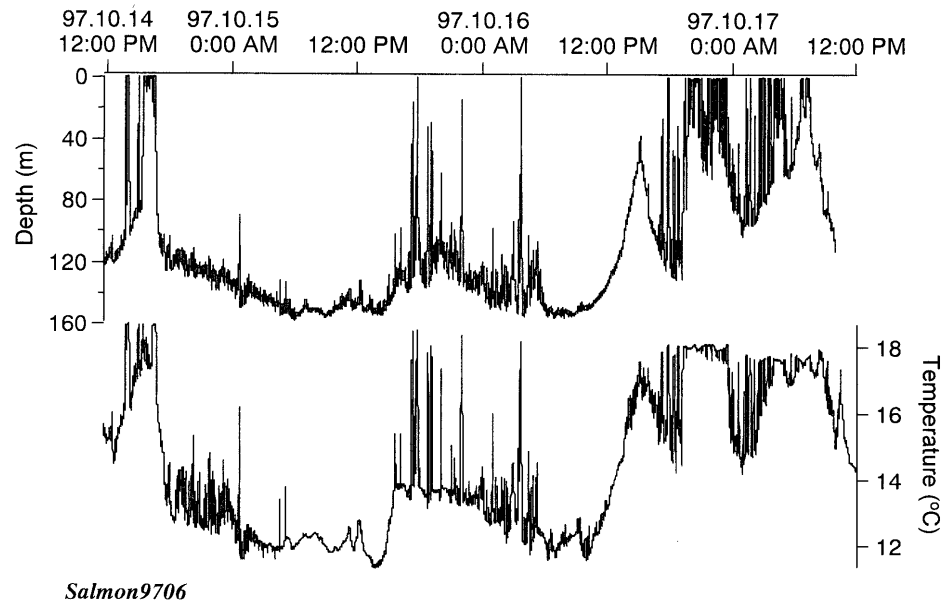

Fig. 2. Typical profiles of swimming depth and ambient temperature of a silver-colored homing adult chum salmon (number 9706) recorded off the Sanriku coast in October 1997.

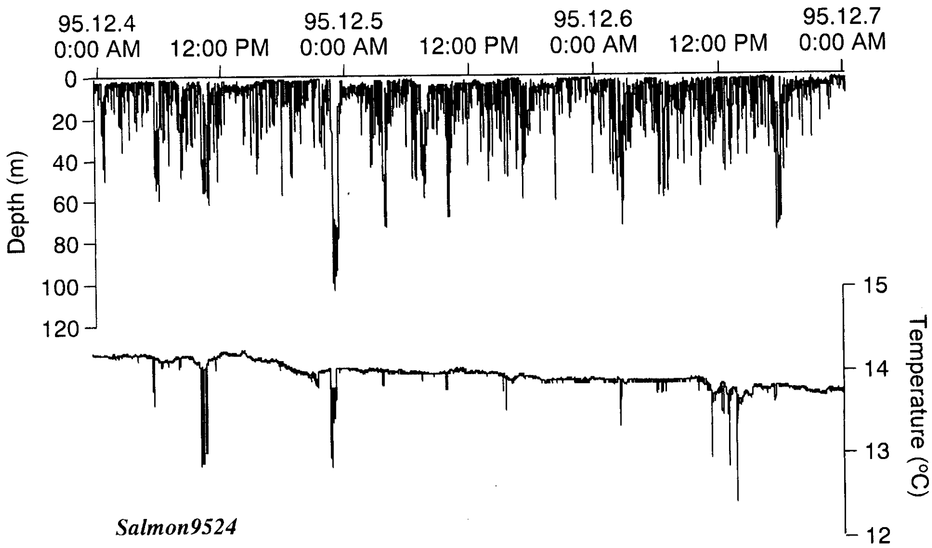

Fig. 3. Typical profiles of swimming depth and ambient temperature of a silver-colored homing adult chum salmon (number 9524) recorded off the Sanriku coast in December 1995.

usually stayed in water shallower than 50 m, making descents and ascents restlessly all through the recording periods. Seawater temperature was thermally mixed over the swimming depth of the salmon. Therefore, the ambient temperature that the salmon experienced was stable compared with that in October. The behavior of salmon in November was intermediate between that recorded in October and December. More detailed individual data on body size, recording period, and behavior of salmon in October, November and December were published in Tanaka (1999) and Tanaka et al. (2000).

As a common index of the thermal condition of the salmon, we calculated the mean value of water temperature that each salmon experienced in the water column shallower than 10 m. The temperatures for the individual salmon ranged from 12.8±0.17°C to 18.9±0.19°C (Mean±S.D.). There was a significant negative relationship between the thermal condition of each salmon and the amount of time spent in shallow water (less than 10 m); salmon spent little time in shallow water when they experienced higher temperatures (Fig. 4). In other words, salmon make deep and longer dives when the surface temperature is high. These data suggest that salmon change their behavior depending on the water temperature and its vertical profile.

As mentioned above, salmon spent much time in deep cool water in October and November. We closely analyzed the depth data to figure out the features of the diving behavior of salmon. A dive was defined as starting when a salmon passed below 10 m and as finishing when it ascended above 10 m. A more detailed method of analysis is presented in Tanaka et al. (2000). Most dives recorded in October and November showed a steady descent and ascent phase to and from a certain depth, with a "dive bottom" where salmon made only small vertical movements. On the contrary, dives in December rarely showed such a dive bottom but were characterized by frequent changes of vertical direction during the course of the dives. The percentage of time devoted to diving behavior was highest in October and lowest in December. In October, it was 66.2±37.8% in 1996 and 72.9±11.1% in 1997. It was 49.3±16.3% in

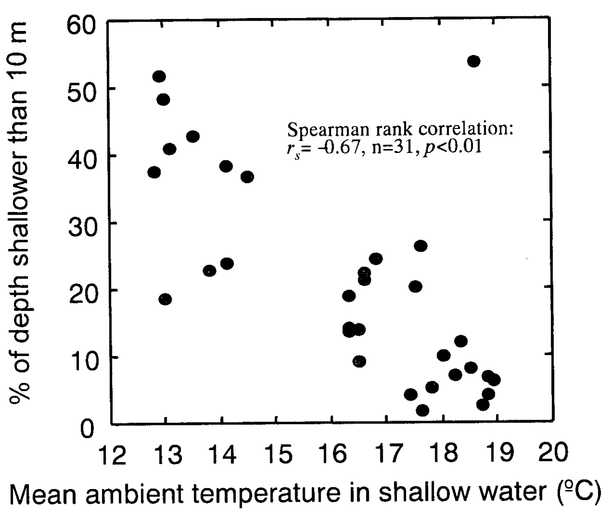

Fig. 4. Relationship between percentage of swimming depth shallower than 10 m and mean ambient temperature in that water column recorded in experiments with silver-colored salmon in 1995 to 1999. Modified from figure 5 in Tanaka et al. (2000), the *Journal of Experimental Biology*, **203**, pp. 1825–1833.

November 1996, and was 23.2±17.0% in December 1995 and 28.5±19.5% in December 1996. The average duration of a dive was also longer in October compared with that in November and December. The mean dive depth of individual salmon was deeper in October and November compared with that in December. For example, in 1996, mean dive depth was 74.7±23.4 to 115.1±22.9 m in October, 87.1±36.0 to 115.5±38.1 m in November, and 21.9±12.7 to 92.1±26.1 m in December. Diving behavior caused salmon to experience a decrease in water temperature. The thermal decrease caused by a diving behavior was defined as the difference between ambient temperature at the start of the dive and mean temperature during the dive. The thermal decrease depended on the hydrographic condition of the sea. For example, the mean thermal decrease of individual salmon ranged from 2.3±1.2°C to 4.9±1.7°C in October 1996. Similar decreases were recorded in the salmon in

November 1996. In contrast, the ambient temperature was almost constant over the swimming depth of salmon in December because of better thermal mixing, and thus salmon experienced very small thermal decreases. There were significant positive relationships between the thermal decrease and dive duration in October and November; salmon prolong a dive with a greater thermal decrease generated by the dive.

The above-mentioned data clearly indicated that the seasonal change in water temperature and its vertical profile transformed salmon behavior drastically from "deep diving" to "shallow swimming". Deep diving is a characteristic behavior in thermally stratified water with higher surface temperature, whereas shallow swimming is a typical behavior in thermally mixed water with lower surface temperature. In previous studies of three species of Pacific salmon using acoustic transmitters (Døving et al. 1985, Quinn et al. 1989, Ruggerone et al. 1990), the salmon preferred only shallow water. In these studies, the seawater was cooler than 15°C and thermally mixed. The conditions were similar to those encountered in our experiments in December. The present results indicate that salmon can modify their behavioral strategy depending on the thermal condition of the sea.

Other factors, such as salinity and water currents, may also change seasonally and affect the salmon behavior. However, effects of these factors on the salmon behavior seem to be very little. Our preliminary study using a data logger that records temperature, depth and salinity indicated that salmon behavior was not affected by the salinity of the ambient water even before the salmon entered into the river. The data reports of the Hydrographic Department, Maritime Safety Agency, Japan show that currents in subsurface water (10, 50 and 100 m deep) usually flow to the south at nearly the same speeds off the Sanriku Coast and the direction and the flow speed do not change synchronously with the thermal conditions.

Our data showed that the ambient temperature of salmon regulates the frequency and duration of diving behavior. Since homing adult salmon have stopped feeding in the study area, the dives are not related to feeding behavior. Instead, we propose that the function of most deep dives is behavioral thermoregulation for energy conservation. The ambient temperature of the salmon decreases steadily with increasing depth below the thermocline. If salmon follow the thermal gradient to lower temperature, they reach the seabed. The flat-shaped dive-bottoms suggest that salmon followed the seabed during deep dives. The frequency distributions of ambient temperature showed that chum salmon did not have a narrow range of preferred temperatures. These data indicate that salmon sought the coolest thermal refuge that they could exploit during their dives. Dives to a thermal refuge cause the salmon to minimize the cumulative effects of ambient temperature, i.e., to minimize their metabolic energy cost. From our calculations using the reported value of resting metabolic rate of sockeye salmon (*O. nerka*; Brett 1973), chum salmon on the sea bottom at 15°C can save approximately 40% of their metabolic energy compared with the cost of remaining in the surface layer at 20°C.

SALMON BEHAVIOR AT THE SURFACE

Salmon frequently returned to the surface in October and November, even though the surface temperature was high. A typical example is shown in Fig. 2. If diving to deep, cool water is beneficial for the salmon in this season, why would salmon return to surface, high-temperature waters so frequently? One possible reason is that directional cues for homing, such as the odor of the natal river water, are more concentrated in the surface waters. The availability of directional cues at the surface has been proposed to explain similar surfacing behavior observed in other salmonid species (Døving et al. 1985, Quinn et al. 1989, Ruggerone et al. 1990). In our study site, there are many small rivers, one of which is the natal river of the salmon used in the study. During the salmon run in the study area, the river water has lower temperature. Because the river water is less dense than the seawater, it stays on the surface where it forms small, cool patches. The salmon may be searching for river water to find their way to the natal river. In order to examine this hypothesis, we studied the salmon behavior at the surface in detail. Figure 5 shows a typical example of such detailed analysis. In this case, the salmon (number 9640) reached the surface at 20:03 h, but it quickly left the surface. At this time, the surface temperature was more than 16°C. Similar behavior was also observed at 20:07 h. After 20:15 h, the salmon encountered the cool covering water whose temperature was less than 16°C. In the cool covering water, the salmon ceased vertical movements and stayed at the surface for several minutes. Next, we analyzed the relationship between the period of time that salmon stayed in the 0–1 m water column and the thermal difference within the 0–3 m water column. The thermal difference, an indicator of the presence of cool covering water, was calculated by subtracting the minimum temperature in the 0–1 m column in each hour from the maximum temperature in the 1–3 m column during the period. As the thermal difference became bigger, the period of time that salmon stay in the 0–1 m column increased significantly. These data strongly support our hypothesis that the salmon are searching for directional cues to their natal rivers at the surface. Thus, there is a trade-off between thermoregulation and obtaining navigational cues in the surface water column. Salmon appear to be more prone to subject themselves to thermal stress when directional cues are available.

MATURATIONAL CONDITION AND BEHAVIOR

In the previous sections, we described the behavior of salmon that have a silver body color. As mentioned above, these fish are still maturing and are expected to spend several weeks more in offshore waters before ascending the river. Our next question is how salmon behave when they reach the final maturation stage but have not found their natal rivers yet. In October 1996, we collected fully matured individuals at the mouth of the Kozuchi River, which runs into Otsuchi Bay, and released them at the mouth of Otsuchi Bay. Detailed individual data on body size, recording period, and the behavior were published in Tanaka (1999). Figure 6 shows a typical pattern of the behavior of fully matured fish. Even though it was in October and the surface temperature was more than 18°C,

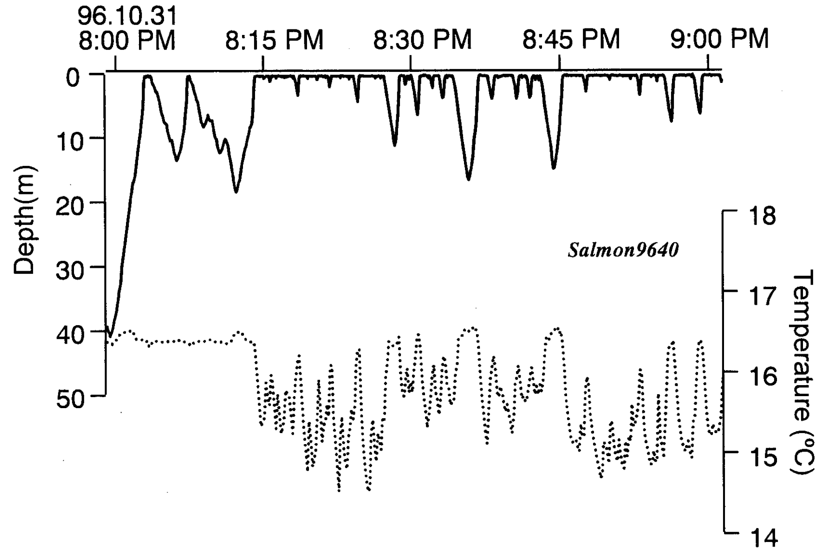

Fig. 5. Time-depth (solid line) and -temperature (broken line) profiles of a silver-colored homing chum salmon (number 9640) recorded off the Sanriku coast in October 1996. Modified from figure 7 in Tanaka et al. (2000), the Journal of Experimental Biology, **203**, pp. 1825–1833.

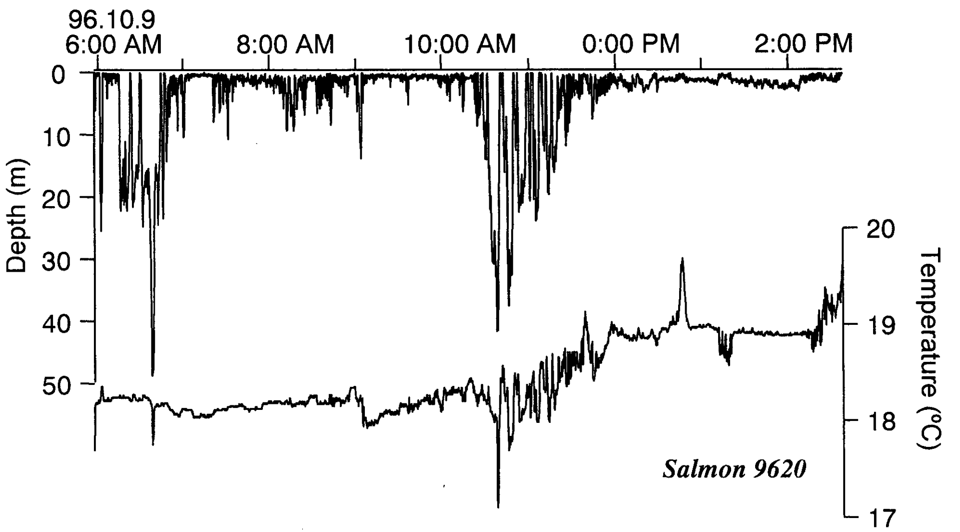

Fig. 6. Typical profiles of swimming depth and ambient temperature of a fully matured chum salmon (number 9620) recorded off the Sanriku coast in October 1996.

fully matured fish did not make long or deep dives as the maturing, silver-colored fish did. Instead, they stayed at depths shallower than 50 m, making restless descents and ascents, just like the salmon in December. Moreover, fully matured fish usually reached the river within several hours. This means they never swam outside of the bay; rather, they swam into the bay toward the river. As we have already mentioned, the purpose of deep diving is to reduce the metabolic energy consumption of salmon, whereas the purpose of surface swimming is to detect the scent of their natal rivers. The present results indicate that salmon change their behavioral priority depending on their maturational condition. Fully matured fish must find their natal river as soon as possible, and thus they must remain in surface waters even when the temperature is high. In addition to these experiments, maturing fish with slight yellow-brown body color were equipped with data loggers and released at the mouth of the Otsuchi Bay in October 2001. These fish were presumed to be slightly more mature than the silver fish, but they had still not reached the ovulation stage. They showed a higher preference for the surface compared with the silver-colored fish, but they still made some long and deep dives. Taken together, these data clearly show the presence of a trade-off between deep diving (in order to thermoregulate) and surface swimming (in order to navigate to the natal rivers), and the trade-off may change depending on the maturational condition of the salmon.

SWIMMING SPEED

The distributions of swimming speeds of each chum salmon showed a broad peak ranging from 0.5 to 1.0 m/sec. The swimming speed rarely exceeded 1.5 m/sec. Swimming speed tended to be lowest in the middle of the night (21:00–03:00 h), and highest at midday (09:00–15:00 h).

The swimming speed of each salmon can tell us the horizontal distance that each fish moved during the study. From the swimming speeds and the rates of change of depth (vertical rate), the horizontal distances that salmon moved per hour were obtained by simple trigonometry. Chum salmon traveled horizontally at 1.5–3.0 km/h. The gross horizontal distance that salmon traveled during the total recording periods were 1.24- to 19.0- fold greater than the net distance between the release and the retrieval points. This data shows that salmon do not migrate immediately to their natal rivers, but undertake extensive horizontal movements. The extremely high ratios of gross to net horizontal distance in some individuals suggest that coastal migrations are not strongly oriented and contain an element of random movements. For more detailed individual data, see Tanaka (1999) and Tanaka et al. (2001).

DIFFERENCES IN DESCENT AND ASCENT MOVEMENTS

Chum salmon utilize a wide range of depth in the Sanriku coastal area during their homing migration. They frequently make vertical movements. Next, we analyzed the energetic aspects of the vertical movements of the salmon. The data logger equipped with speed, depth, and temperature monitors enabled us to compare swimming speed and vertical rate between descent and ascent movements. A new data logger that was equipped with acceleration monitors along with speed, depth and temperature monitors was also applied. This data logger enabled us to compare several characteristics between the descent and ascent movements, including the body angle, tail beat frequency, amplitude of the tail thrust, vertical rate and swimming speed.

The individual vertical descent rates (0.26 ± 0.07 to 0.37 ± 0.11 m/sec) were significantly faster than the ascent rates (0.22 ± 0.07 to 0.29 ± 0.11 m/sec). The swimming speeds were similar in descent (0.67 ± 0.12 to 1.04 ± 0.15 m/sec) and ascent (0.66 ± 0.43 to 1.03 ± 0.19 m/sec). However, the tail beat frequencies per 1 m depth change in the descent phase (2.9 ± 1.8 and 6.2 ± 1.6) were significantly lower than those in the ascent phase (7.8 ± 1.7 and 9.6 ± 1.9). The amplitudes of tail thrust in the descent phase (2.5 ± 0.6 and 3.0 ± 1.2 m/sec^2) were also smaller than those in the ascent phase (4.4 ± 0.6 and 4.5 ± 1.2 m/sec^2). The descent angles (-25.3 ± 5.3 and -22.9 ± 4.2 degree) were significantly steeper than the ascent angles (19.7 ± 7.2 and 18.3 ± 3.8 degree). For more detailed individual data, see Tanaka et al. (2001).

These data clearly indicate that salmon have negative buoyancy through the course of their vertical travel, and as a result, they use more energy during the ascent. In other words, they can descend passively with a lower locomotive energy, whereas they need more energy for the ascent movement. Chum salmon have a swim bladder with a connection to the gut. They are believed to be able to change the volume of the swim bladder. However, the present results suggest that the volume of gas in the swim bladder of chum salmon is just enough to achieve neutral buoyancy only in the surface water. As a consequence, chum salmon are negatively buoyant all through the course of their vertical travel, since the hydrostatic pressure decreases the volume of the swim bladder and reduces the buoyancy when they descend from the surface. Wittenberg (1958) reported that rainbow trout can secrete gas into the swim bladder but the replacement of emptied swim bladder was 30–55% complete at 7 days and 32–100% complete at 13 days. If chum salmon have a similar ability of gas secretion, then a chum salmon that was neutrally buoyant at the surface and that dived to a depth of 10 m and remained at that depth would take 7 days or more to recover its neutral buoyancy by gas secretion. Therefore, such a volume-control mechanism of the swim bladder has little ability to change the buoyancy of the salmon in their vertical movements. These results suggest that the energy cost for deep diving cannot be negligible. It seems that chum salmon have to stay more than several hours in a thermal refuge in order to overcome the debt from the cost of locomotion. This can explain why salmon did not make a series of short and deep dives, but instead, made long and deep dives in thermally stratified waters.

CONCLUSION AND FUTURE PERSPECTIVES

The present review describes the behavior of homing adult chum salmon off the Sanriku coast. Their behavior changes from deep diving to surface swimming depending on the hydrographic structure of the coastal waters. Seawater temperature has a strong effect on their behavior. Deep diving in thermally stratified water is a type of behavioral thermoregulation that reduces metabolic energy cost, whereas surface swimming helps the salmon to locate their natal rivers. Moreover, there is a trade-off between deep diving and surface swimming, and the trade-off may change depending on the maturational condition of the salmon. An analysis of the vertical movements of the salmon indicated that salmon are negatively buoyant throughout the dive, and thus, the energy cost for deep diving cannot be negligible. This can be the reason why chum salmon made very long dives for energy conservation.

All these data clearly indicated that the salmon were extremely well adapted to thermally stratified water with a high surface temperature. However, little is known about the physiological effects of high temperature on the chum salmon returning to Sanriku area. Our results show that salmon need to swim at the surface in order to find their natal rivers, even if high temperature may have adverse physiological effects on them. The effects of such high temperature on the eggs and sperm of the salmon should be evaluated in the future, because germ cells are generally highly susceptible to physiological stress. Laboratory experiments are needed to evaluate the effect of temperature on the germ-cell physiology.

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