

## BEHAVIOURAL THERMOREGULATION OF CHUM SALMON DURING HOMING MIGRATION IN COASTAL WATERS

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### Summary

Homing Pacific salmon are suggested to utilise directional cues in shallow water while migrating in coastal waters. Since salmonids are typical cold-water fish, they may have to cope with warm surface water while gathering directional information. We studied behavioural thermoregulation of 31 free-ranging chum salmon *Oncorhynchus keta* using micro data loggers off the Sanriku coast from early October to December. The surface water temperature was approximately 20 °C in early October and decreased to approximately 12 °C in December. The seasonal change of water temperature transformed the behaviour of salmon markedly from deep diving to shallow swimming. In October, salmon frequently dived to depths exceeding 100 m. Duration of deep dives tended to be prolonged as the thermal difference between sea surface and bottom water increased. The results indicated that salmon sought the coolest thermal refuge

that they could exploit by vertical movement. Thermal refuge could be a way for salmon to minimise metabolic energy cost; however, salmon repeatedly returned to the surface water column. We found a positive correlation between surface swimming of salmon and the presence of cool covering water, which could contain river waters. This suggests that salmon tend to be risk-prone when subjected to a high concentration of directional cues. Salmon in December spent most of their time in shallow water. These findings suggest that salmon adjusted their behavioural strategy with the hydrographic structure of the sea in order to achieve a balance between acquiring directional cues and behavioural thermoregulation.

Key words: chum salmon, *Oncorhynchus keta*, thermoregulation, behavior, vertical movement, data logger, migration.

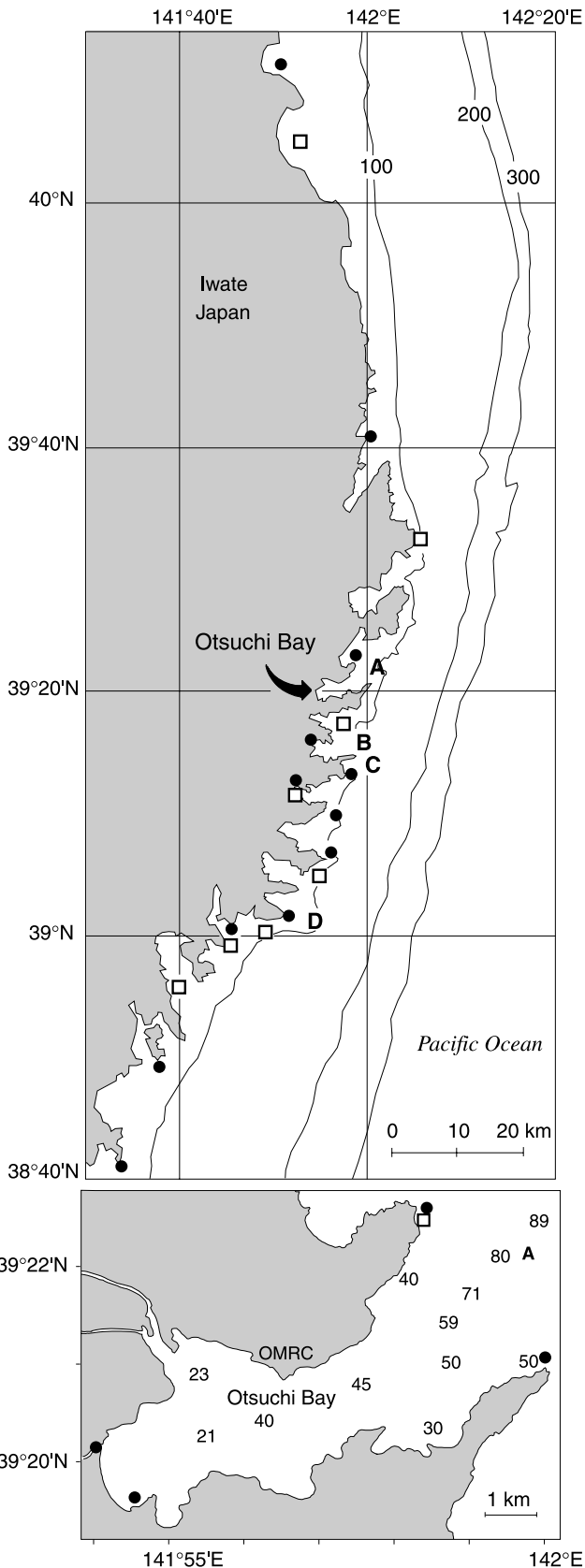
### Introduction

Pacific salmon have a typical anadromous life history. They are born in a river, mature in the ocean, and return to the natal river to spawn. It is generally accepted that the directional cue for homing salmon in the river system is the imprinted odour of their spawning grounds (Hasler et al., 1978). The mechanisms of oceanic migration have not been determined and those of coastal waters may involve elements of both oceanic and riverine phases (Quinn et al., 1989). The behaviour of salmon in coastal waters has been intensively studied by acoustic tracking, to evaluate various hypotheses on navigation mechanisms (Døving et al., 1985; Quinn, 1988a; Quinn et al., 1989; Ruggerone et al., 1990). Based on these reports, homing individuals generally show a preference for shallow water and their swimming depth is guided by vertically stratified hydrographic features (Døving et al., 1985; Quinn et al., 1989; Ruggerone et al., 1990). These findings suggest that homing salmon might use a directional cue found in the shallow water that is absent in the deeper water column. By contrast, off the Sanriku coast, Northern Honshu Island, Japan, there are traditional fisheries for homing chum salmon *Oncorhynchus keta* using gill nets and trawls, which are set at depths of 100 m

or more. This observation suggests that homing salmon also spend considerable time in deep water, but there is little scientific information concerning the character and function of such deep swimming of Pacific salmon, including chum.

The chum salmon is one of seven species of North Pacific *Oncorhynchus*. Like other salmonids, chum salmon is a typical cold-water fish and its upper lethal temperature does not extend above 24 °C (Schmidt-Nielsen, 1990). Welch et al., (1995) reported that the critical temperature, which defines the southern boundary of the Pacific distributional area, is 10.2 °C. Honshu Island in Japan is the southernmost spawning ground of Pacific salmon (Kaeriyama, 1989). The returning season of chum salmon is generally from 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.

Therefore, one possible reason for the observed deep swimming of salmon could be their avoidance of warm water, but how homing Pacific salmon select a preferred depth in warm and thermally stratified sea water is poorly understood. The objective of the present study was to investigate the behavioural strategy of homing chum salmon off the Sanriku



coast and, in particular, to examine how salmon manage their time to achieve a balance between avoidance of warm water and access to directional cues, since homing salmon have a

Fig. 1. Maps showing the study site off the Sanriku coast, Japan. The lower panel shows the Otsuchi Bay in more detail. Homing adult chum salmon were caught and released with data loggers attached at point A (3 October 1996, 29 October 1996 and 14 October 1997), point B (1 December 1995), point C (1 December 1995 and 5 December 1996) and point D (5 December 1995). Filled circles indicate the places where salmon released at point A were recovered and open squares show locations where other fish were retrieved. Numbers indicate sea depth and lines show 100, 200 and 300 m contours.

limited time in which to reach the mouth of their natal rivers before their final maturation. The behavioural strategy of homing adults is expected to alter depending on the concentration of directional cues, or the presence of any thermal refuge.

To study the swimming behaviour and ambient temperatures of homing chum salmon, we used a newly developed micro data logger. In previous studies on salmon behaviour using acoustic transmitters (Døving et al., 1985; Quinn et al., 1989; Ruggerone et al., 1990), difficulties in tracking limited the study site to semi-closed systems, the study duration to a few days or less, and the number of observations (Boehlert, 1997). Therefore, studies on the behaviour of free-ranging salmon in open systems are scarce. Data logger tagging makes it possible to study the swimming behaviour of free-ranging fish under various environmental conditions and less labour intensity compared with telemetry tracking methods, although the position of the animal is not known. This work was pioneered with seals, and recent reductions in the size of data loggers has led to a proliferation of studies on smaller aquatic tetrapods and birds (Kooyman et al., 1992). Applications of this method to studies on fish biology are now beginning. Chum salmon are suitable subjects for a data logger study, since they will continue homing migration with an external micro data logger attached (Tanaka et al., 1998).

### Materials and methods

The behaviour of homing adult chum salmon *Oncorhynchus keta* (Walbaum) was studied off the coast of Sanriku in the northern part of Honshu Island, Japan (Fig. 1), in early December 1995, early October 1996, late October to early November 1996, December 1996 and early October 1997. On the Sanriku coast there is a rich stock of chum salmon, resulting from about 30 salmon hatcheries in rivers. Much information on the general behaviour and physiology of these salmon has been accumulated. In the study area, returning chum salmon that group off the coast are expected to ascend their natal rivers within a few weeks. It is commonly observed that the stomachs of these chum salmon are empty, so they seem to have already stopped feeding in our study area.

Except in December 1995 and December 1996, the studies were carried out in Otsuchi Bay, which has a width of 3.5 km at the bay mouth and a depth of less than 90 m. The Otsuchi, Kozuchi and Unosumai rivers flow into the bay. The distance

from the river mouths to the bay mouth is about 6.5 km. The chum salmon used in this study were hatchery-reared. All fish except for those in the December experiments were caught by a trap net in the Otsuchi Bay at dawn or around noon. Then the salmon were transferred into the outdoor tank of the Otsuchi Marine Research Center (OMRC), Ocean Research Institute, University of Tokyo, located on Otsuchi Bay. Individual fish were lightly anesthetized using 2-phenoxy ethanol, and total length and body mass were measured. 2-phenoxy ethanol appears to have no adverse effect on the homing of Pacific salmon (Quinn, 1988b). 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 loggers were printed on them. Each fish was transferred to a recovery tank and allowed 2–12 h to recover from anesthesia and surgery, before being transferred to the center of the bay mouth (point A in Fig. 1) and released.

Generally in December, salmon trapped in Otsuchi Bay are in their final stage of maturation (Hirano et al., 1990) and supposed to have only a few days left before ascending their natal rivers. In December 1995 and December 1996, therefore, chum salmon fished by a long line outside the bay were used. In order to exclude as much variation in the physiological state of the salmon as possible, in both series of experiments we selected silver-coloured individuals, which were expected to be at same stage of sexual maturation. At sea, they were lightly anesthetized by 2-phenoxy ethanol, their total lengths measured, and data loggers attached as described above. Fish were allowed approximately 60 min to recover from anesthesia and surgery and released into the sea near the capture site (points B, C and D in Fig. 1).

We used several kinds of micro data loggers (Little Leonard Co. Ltd., Tokyo, Japan), which record depth and temperature simultaneously. Each type of logger was cylindrical in shape, 62–90 mm in length and 19–20 mm in diameter, weighed 30–42 g in air, 9–13 g in sea water, and had 0.5 or 1.0 MB of flash memory. Resolution of the depth channel was 0.05 m and of the temperature channel, 0.02 °C. Maximum range of the depth channel was 200 m. Accuracy of the depth channel was  $\pm 0.5$  m, and of the temperature channel,  $\pm 0.1$  °C. Sample rate,

which was programmed for each salmon, varied from 1 to 5 s in the depth channel and 5 to 15 s in the temperature channel. Fishermen in the Sanriku coast usually haul their set nets twice a day and transfer the salmon onto a boat. From the time-depth data recorded in the logger, we could easily determine when the salmon were transferred onto a boat. To exclude data from salmon behaviour whilst constrained in a net, we omitted from our analysis any data recorded after the previous net-hauling event.

All values are presented as means  $\pm$  s.d. unless noted otherwise, and statistical significance was set at  $P=0.05$ .

## Results

### General features

Locations of logger release and recovery are shown in Fig. 1. A total of 69 homing adults were released with data loggers, and 35 loggers were retrieved by commercial fishermen or researchers. Unfortunately, some loggers did not function properly for unknown reasons, and we finally obtained data from 31 individuals (four in early December 1995, five in early October 1996, eight in late October to early November 1996, five in December 1996, and nine in early October 1997), consisting of 16 males and 15 females. Mean fork length was  $64.3 \pm 4.6$  cm for all individuals and mean body mass was  $3186 \pm 533$  g for 22 salmon in October and November. Mean data recording length was  $3.2 \pm 2.4$  days and the longest record was 9.98 days.

The seasonal change in water temperature transformed the behaviour of salmon drastically from deep diving to shallow swimming. A section from the record of one fish, number 9602, recorded in October 1996, showed the typical pattern of changes in swimming depth and ambient temperature for salmon in October (Fig. 2). Salmon dived to over 100 m and stayed in the deep water for several hours. Some individuals even reached depths beyond the measurement range of the logger, i.e. more than 200 m. However, salmon repeatedly came back to the surface. Sea water is thermally stratified, and thus some fish experienced a variation of nearly 10 °C in their ambient temperature, even within a single descent or ascent. In

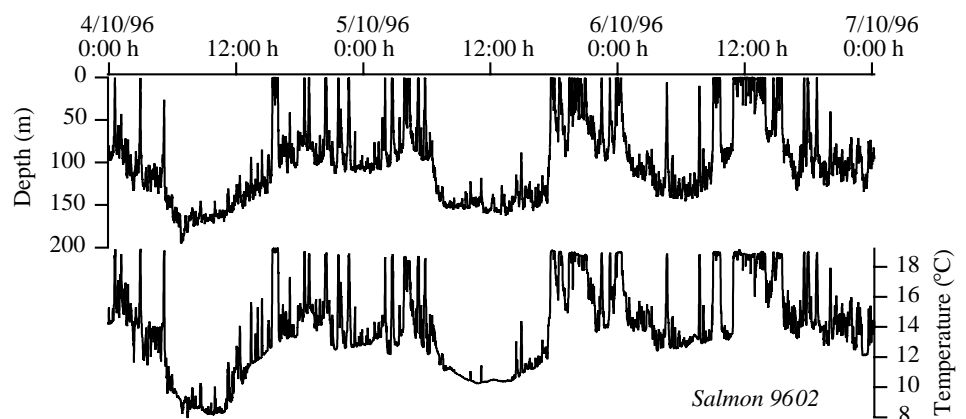


Fig. 2. Typical profiles of swimming depth and ambient temperature of homing chum salmon number 9602 off the coast of Sanriku in early October 1996.

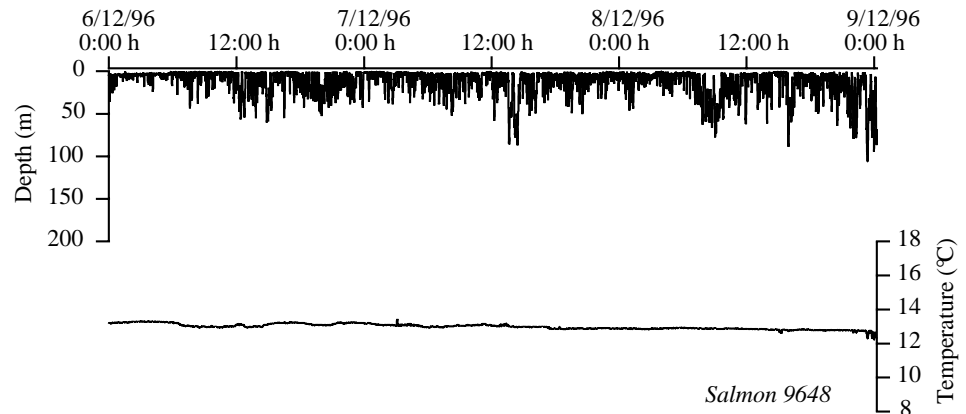


Fig. 3. Typical profiles of swimming depth and ambient temperature of homing chum salmon number 9648 off the coast of Sanriku in early December 1996.

contrast to the behaviour in October, salmon in December rarely showed long, deep dives, as demonstrated by the record of fish number 9648 (Fig. 3). Salmon usually stayed in water shallower than 50 m, but vertical movement occurred continuously all through the recording periods. Ambient temperature remained almost constant over the swimming depth of the salmon. The mean descent rate and ascent rate of each salmon ranged from  $0.18 \pm 0.07$  ( $N=61$ ) to  $0.36 \pm 0.12$   $\text{m s}^{-1}$  ( $N=65$ ) and from  $0.13 \pm 0.05$  ( $N=73$ ) to  $0.31 \pm 0.07$   $\text{m s}^{-1}$  ( $N=66$ ), respectively. We could not find any consistent link in depth and temperature data with gender of individuals.

#### *Swimming depth and ambient temperature*

Fig. 4 shows typical examples of the frequency of swimming depths with the vertical profile of ambient temperature for salmon in October, November and December. In October and November, vertical profiles of temperature were stable in shallow water and then decreased steadily with depth. A thermocline was built up in the water column shallower than 50 m in October and moved deeper as the surface water temperature got cooler later in the year. Swimming depths of salmon showed bimodal frequency distributions. Salmon spent little time within the shallow and isothermal water column except in the 0–10 m range. In addition to this sharp peak at 0–10 m depth, the frequency of swimming depth showed a broad peak at 50–180 m in October and at 90–170 m in November. The frequency of swimming depths began to increase at approximately the depth where ambient temperature began to decrease. The ambient temperature varied among individuals depending on their vertical movement. Mean ambient temperatures of each of five salmon in October 1996 ranged from  $13.4 \pm 2.3$  °C ( $N=31193$ ) to  $18.5 \pm 0.6$  °C ( $N=3225$ ),  $12.7 \pm 3.0$  °C ( $N=100107$ ) to  $17.3 \pm 1.0$  °C ( $N=4913$ ) for nine salmon in October 1997, and  $13.6 \pm 2.3$  °C ( $N=7489$ ) to  $15.9 \pm 1.2$  °C ( $N=1508$ ) for eight salmon in November 1996, while the shallow water temperature of individuals was almost constant in each group of salmon (see below). In December, salmon spent most of their time at depths between 0–10 m. Ambient water was thermally mixed over the swimming depth of the salmon, and mean ambient temperature ranged from  $13.6 \pm 0.27$  °C ( $N=57810$ ) to  $14.5 \pm 0.19$  °C ( $N=11248$ ) for four salmon in

December 1995 and  $12.7 \pm 1.0$  °C ( $N=21491$ ) to  $13.1 \pm 0.29$  °C ( $N=9634$ ) for five salmon in December 1996, respectively.

To remove the effect of thermal stratification, we analyzed the mean value of shallow water temperature (shallower than 10 m) as a common index of the thermal condition of the salmon. The mean value for each salmon ranged from  $12.8 \pm 0.17$  °C ( $N=13161$ ) to  $18.9 \pm 0.19$  °C ( $N=2957$ ). The relation between percentage of swimming depth shallower than 10 m and the shallow water temperature is plotted in Fig. 5. The amount of time salmon spent in shallow water increased markedly with decreasing shallow water temperature (Spearman rank correlation:  $r_s = -0.67$ ,  $N=31$ ,  $P < 0.01$ ).

#### *Diving behaviour*

In thermally stratified water in October and November, salmon spent much of their time in deep water. We re-analyzed the depth data to clarify the features of swimming behaviour in deep water, which we refer to diving behaviour. Diving behaviour was defined as starting when a descending salmon passed below 10 m and finishing when it ascended to 10 m. For simplification, we restricted our analysis to diving behaviours longer than 1 h. Dive depth was defined as mean value of swimming depth during diving behaviour. To exclude the phases of descent and ascent, data within 10 min after the start and before the end point of each dive were omitted from the analyses. Thermal decrease from the sea surface caused by the diving behaviour was calculated as the difference between ambient temperature at the start time and mean temperature during the diving behaviour.

In total, 275 diving behaviours were recorded from 31 individuals. Most dives recorded in October and November showed a steady descent and ascent phase to and from a certain depth, where salmon made only small vertical movements for several hours. Some deep dives even had a 'dive bottom' with almost no vertical changes for minutes. In contrast, dives in December were characterized by frequent changes of vertical direction for their entire duration. Deep dives were recorded less frequently around midnight. Dives deeper than 150 m or longer than 15 h were rare. The longest dive duration was 1840 min by fish number 9613 in October 1996, whereas number 9605 was the only fish that did not make any dives during its recording periods, which lasted 8.9 h. The mean

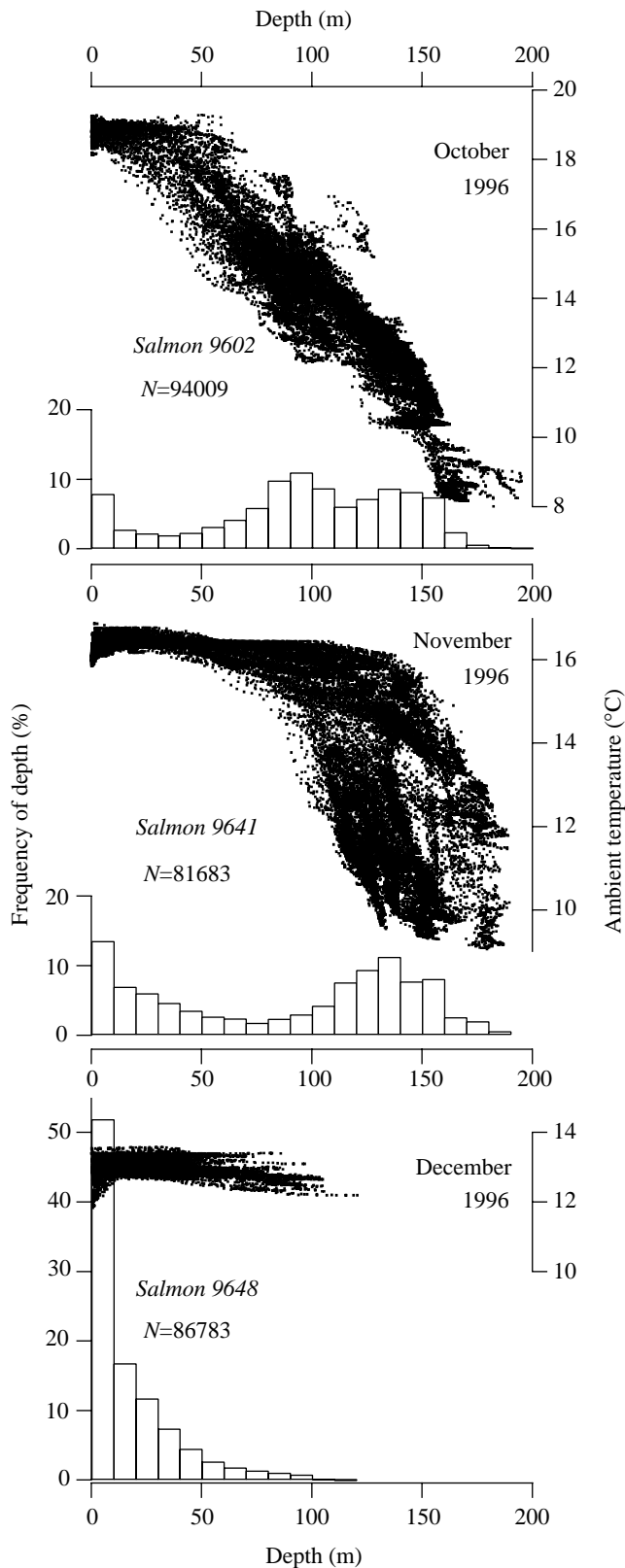


Fig. 4. Frequency of swimming depth with vertical profile of ambient temperature of homing chum salmon during total recording periods for (A) fish number 9602 in October 1996, (B) fish 9641 in November 1996 and (C) fish 9648 in December 1996.

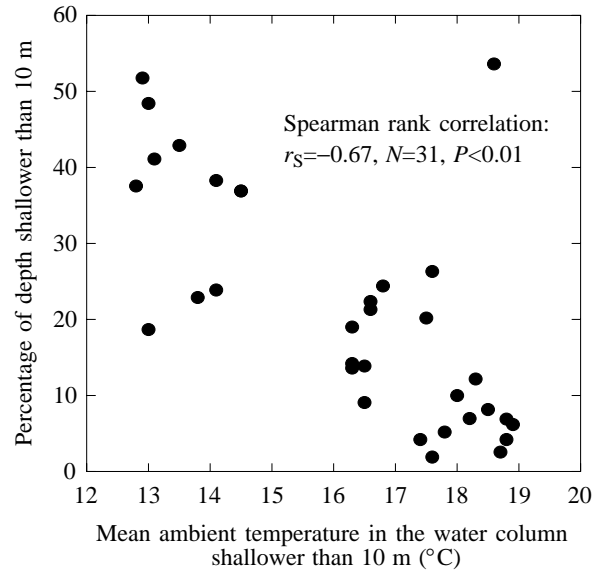


Fig. 5. Relationship between percentage of swimming depth shallower than 10 m and mean ambient temperature in that water column during the total recording periods for 31 homing chum salmon off the coast of Sanriku.

percentage of time salmon spent in dives was  $66.2 \pm 37.8\%$  ( $N=5$  in 1996) and  $72.9 \pm 11.1\%$  ( $N=9$  in 1997) in October,  $49.3 \pm 16.3\%$  ( $N=8$ ) in November, and  $23.2 \pm 17.0\%$  ( $N=4$  in 1995) and  $28.5 \pm 19.5\%$  ( $N=5$  in 1996) in December.

The mean dive depth in October ranged from  $74.7 \pm 23.4$  ( $N=5$ ) to  $115.1 \pm 22.9$  m ( $N=9$ ) in 1996 and  $70.8 \pm 36.9$  ( $N=17$ ) to  $109.5 \pm 37.3$  m ( $N=8$ ) in 1997, and in November 1996 it varied from  $87.1 \pm 36.0$  ( $N=9$ ) to  $115.5 \pm 38.1$  m ( $N=16$ ). In contrast to deep dives recorded in October and November, in December salmon made few dives deeper than 100 m. The mean dive depths ranged from  $63.4 \pm 27.1$  ( $N=6$ ) to  $82.5 \pm 21.7$  m ( $N=10$ ) in 1995 and  $21.9 \pm 12.7$  ( $N=5$ ) to  $92.1 \pm 26.1$  m ( $N=11$ ) in 1996. Salmon appeared to dive for longer in October than in other months. In October, the mean dive duration for each salmon varied from  $170.6 \pm 91.9$  ( $N=5$ ) to  $525.6 \pm 567.2$  min ( $N=9$ ) in 1996 and  $150.2 \pm 97.9$  ( $N=10$ ) to  $509.2 \pm 524.6$  ( $N=7$ ) min in 1997. In November and December, most dive durations were within the range 60–120 min. Mean dive duration for each salmon in November ranged from 85.0 ( $N=1$ ) to  $361.1 \pm 518.7$  min ( $N=10$ ) and those in December varied from  $78.3 \pm 35.2$  ( $N=6$ ) to  $128.3 \pm 95.1$  min ( $N=23$ ) in 1995 and from  $66.4 \pm 5.9$  ( $N=3$ ) to  $220.2 \pm 68.6$  min ( $N=3$ ) in 1996. Overall, dive depth did not appear to correlate systematically with dive duration. For example, in 1996, dive durations of salmon in October were significantly longer than those of salmon in November (Mann–Whitney  $U$  test:  $U=927.5$ ,  $N1=41$ ,  $N2=60$ ,  $P < 0.05$ ), although there was no significant difference among their dive depths ( $U=978$ ,  $N1=41$ ,  $N2=60$ ,  $NS$ ).

The extent of the thermal decrease differed from dive to dive according to the thermal environment which each individual experienced. In October, salmon experienced a thermal

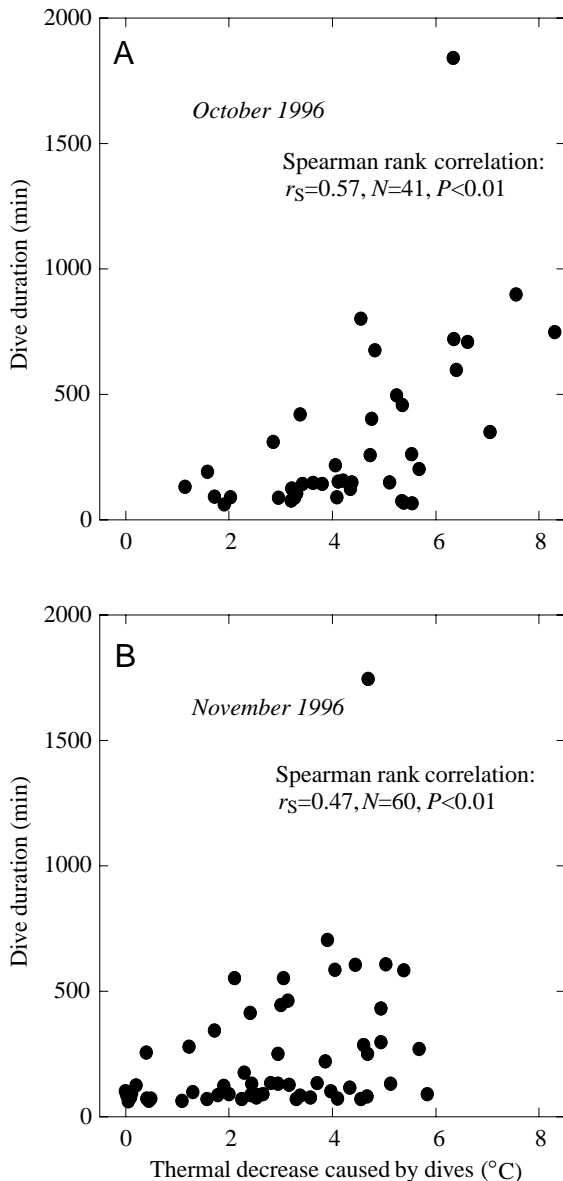


Fig. 6. Relationship between dive duration and thermal decrease from the surface during dives of four salmon in October 1996 (A) and eight salmon in late October to early November 1996 (B).

decrease of  $2.3 \pm 1.2$  °C ( $N=5$ ) to  $4.9 \pm 1.7$  °C ( $N=9$ ) in 1996 and  $1.6$  °C ( $N=1$ ) to  $4.7 \pm 2.4$  °C ( $N=18$ ) in 1997. Some dives of salmon in November did not result in any detectable thermal decrease, because of better thermal mixing. The mean thermal decrease caused by a dive was  $1.4 \pm 1.5$  °C ( $N=9$ ) to  $4.0 \pm 1.5$  °C ( $N=7$ ) for eight salmon in November 1996. As already mentioned (Fig. 3), the ambient temperature was almost constant over the swimming depth in December, and the thermal decrease was very small. Fig. 6 illustrates the relationship between the dive duration and the thermal decrease in October and November in 1996. All the dives obtained in each month were plotted together, because single individuals did not perform enough dives to allow statistical testing. Salmon tended to prolong a dive with a greater thermal

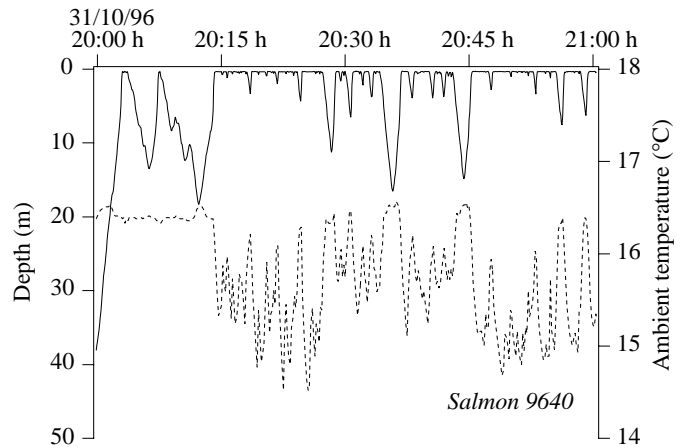


Fig. 7. Time–depth (solid line) and temperature profile (broken line) of a homing chum salmon (fish 9640) off the coast of Sanriku. Before 20:15 h, there was no detectable cool covering water and salmon quickly left the surface to dive. Thereafter, salmon encountered the cool covering water and ceased vertical movements for periods of minutes in the top surface.

decrease generated by the dive (four salmon in October 1996, Spearman rank correlation:  $r_s=0.57$ ,  $N=41$ ,  $P<0.01$ ; eight salmon in November 1996,  $r_s=0.47$ ,  $N=60$ ,  $P<0.01$ ). A similar relationship was also observed in October 1997 (nine salmon,  $r_s=0.62$ ,  $N=101$ ,  $P<0.01$ ).

#### Cool covering water

In October and November, the data loggers recorded cool water masses that covered the warmer sea surface in patches. Salmon stopped their vertical movement for minutes in such cool water masses (Fig. 7). This suggests that cool covering water could play a significant role in drawing salmon to the surface. To test this hypothesis, we analyzed the relationship between the percentage of swimming depth in the 0–1 m water column and the presence of cool covering water. As an index of the presence of cool covering water, we calculated the thermal difference within the surface column by subtracting the minimum temperature recorded in the 0–1 m water column each hour from the maximum temperature in 1–3 m water column during that period. Fig. 8 shows the observed relationship for five salmon in October 1996. The correlation was significantly positive (Spearman rank correlation:  $r_s=0.50$ ,  $N=92$ ,  $P<0.01$ ). There was significant correlation also in November 1996 ( $r_s=0.56$ ,  $N=242$ ,  $P<0.01$ ) and in October 1997 ( $r_s=0.64$ ,  $N=231$ ,  $P<0.01$ ).

#### Discussion

During their homing migration in thermally stratified water, chum salmon made remarkably deep dives, which caused a rapid and wide change in their ambient temperature. This wide-scale depth occupation of chum salmon contrasts sharply with the simple preference of other salmonids for shallow water that has been observed in coastal waters cooler than approximately

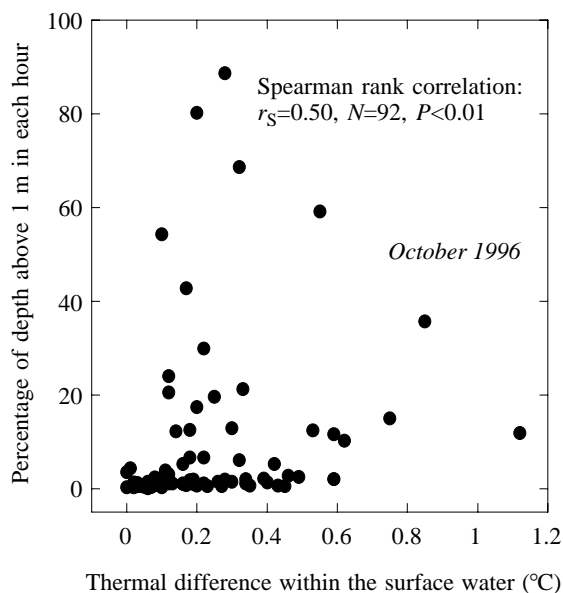


Fig. 8. Relationship between percentage of swimming depth above 1 m in each hour and thermal difference within the surface column (0–3 m deep) for five salmon in October 1996.

15 °C (Døving et al., 1985; Quinn et al., 1989; Ruggerone et al., 1990). Also, chum salmon spent most of their time in shallow water in cool and thermally mixed water. This finding suggests that the behaviour of salmon shows wide variation in a wide range of ambient temperature, even in the final phase of homing migration.

Our data indicate that the ambient temperature of salmon controls the frequency and duration of diving behaviour, which raises the question of its utility. Observed dives are unrelated to feeding behaviour, because chum salmon stop feeding during their homing migration (Hasler et al., 1978). Both diving depth and duration were strongly correlated with the vertical features of ambient temperature. The ambient temperature of salmon decreased steadily with increasing depth below the thermocline. If salmon followed the thermal gradient towards lower temperature, they inevitably reached the sea bed. Within 20 km of the coast off Sanriku, the depth of the sea is less than 200 m. The flat-shaped 'dive bottom' observed in some cases supported the hypothesis that salmon followed the sea bed during deep dives. These results suggest that chum salmon sought the coolest thermal refuge that they could exploit by their vertical movement. Thermal refuge can lead to salmon minimizing the cumulative effects of ambient temperature, i.e. minimizing metabolic energy cost. Thus, we conclude that the function of most deep dives is behavioural thermoregulation for energy conservation. Healey (1986) speculated on the reproductive advantages of large size in Pacific salmon; they were: (1) size domination when competing for mates or nest sites, (2) production of large size eggs and (3) deeper, better-protected nests. In addition, Van den Berghe and Gross (1986) demonstrated the correlation between fish size and survival time at the spawning grounds in

coho salmon *O. kisutch*, and suggested that larger size would increase the chance of successful spawning. Conservation of metabolic energy is the only possible strategy for homing salmon to minimize a decrease in body size because they have stopped feeding.

Metabolic studies of Pacific salmon have concentrated on sockeye salmon *O. nerka*. The estimated resting metabolic rate of a 3.0 kg sockeye is 136.4 mg O<sub>2</sub> h<sup>-1</sup> at 15 °C and 219.8 mg O<sub>2</sub> h<sup>-1</sup> at 20 °C (Brett, 1973). In order to make our calculations simple and comprehensible, we extrapolated these values to chum salmon of the same body mass. If salmon remained still, it can be estimated that staying in the sea bottom at 15 °C could save approximately 40% of their metabolic energy compared to the cost of remaining in 20 °C surface water. It may also be possible for salmon to use favourable currents for migration in sub-surface water to reduce their cost of transport. Data reports published by the Hydrographic Department, Maritime Safety Agency, Japan, however, show that currents in sub-surface water (10, 50 and 100 m deep) usually flow to the south at nearly the same speeds off the Sanriku coast. The present study and traditional tag experiments in the region (Ishida et al., 1988) show that chum salmon travel both southward and northward before arrival at the natal river. These facts suggest that sub-surface currents have different effects on different individuals in the Sanriku coastal area. In addition, the data reports do not show the existence of currents that change in direction or flow speed synchronously with the thermal conditions. Therefore, the cost of transport saved by utilizing sub-surface currents could explain the deep swimming of chum salmon only in exceptional conditions.

Another possible adaptive significance of a series of deep dives could be regulation of pre-spawning holding temperature, which can be critical for offspring survival (Berman and Quinn, 1991). There is evidence that the upper temperature thresholds for normal embryonic growth in chinook *O. tshawytscha* and sockeye salmon lie between 14.2 °C and 15.5 °C (Weatherley and Gill, 1995). Chum salmon could decrease such a risk of deterioration of body condition by a series of deep dives to the cold bottom water.

Diel vertical migrations of fish or zooplankton are broadly observed phenomena under natural conditions. Gliwicz (1986) compared vertical migration of zooplankton among different conditions of predator evidence. He suggested that migratory behaviour should be favored only in habitats in which both the risk of predation and the resource concentration were significantly higher in the upper water column than in the lower one. In the present study, we found that the risk of deterioration of body condition must be higher in the upper water column, as discussed above; however, chum salmon showed a preference toward the sea surface even in thermally stratified water with high surface temperature. Thus, in thermally stratified water, there should exist a trade-off between surface swimming and deep diving. One possible adaptive significance of surface preference could be the concentration of directional cues for homing individuals, as suggested for other salmonid

species (Døving et al., 1985; Quinn et al., 1989; Ruggerone et al., 1990). At our study site, there are many small river systems, one of which is the natal river of each fish used in the study. River water is cooler but lighter than sea surface water because of its low salinity in our experimental seasons. The cool water masses recorded at the sea surface must be the water draining from the river system. We found a positive correlation between surface swimming of salmon in the 0–1 m column and the presence of cool covering water, which suggests that salmon tended to be risk prone when exposed to a high concentration of directional cues.

In the surface water, chum salmon could also use celestial cues such as the sun, moon and stars for migratory orientation. We analyzed the relationships between frequencies of surface swimming and time of day, weather and age of the moon, but could not find any clear relationships between them. Thus, celestial cues may not be so important for the chum salmon that have already arrived at the coastal area, but may be more important for the salmon that are migrating in the open ocean.

In addition, we found that swimming behaviour at the surface has a conspicuous feature: restless vertical movement even in the thermally mixed isothermal condition. Ishida et al. (1988) also recorded similar features of swimming behaviour of chum salmon off the Sanriku coast. Compared with other species of homing salmon, the vertical movement of the chum salmon off the Sanriku coast is distinctive in its amplitude. Quinn et al. (1989) found that homing sockeye salmon remained in a narrow depth range for long periods, interspersed with brief dives and ascents. Atlantic salmon *Salmo salar* made small vertical movements, with sudden large ones (Døving et al., 1985). Steelhead trout *O. mykiss* spent, on average, 72% of their time in the top 1 m (Ruggerone et al., 1990). A river system such as the Fraser River, which is a sockeye salmon study site, generates dilute domains that may extend several hundred kilometers from the river mouth (Quinn et al., 1989). If there was a single major stream draining into the sea, salmon could follow the gradient of the odour straight to the mouth of the river. In such a case there should be no need for continuous vertical movement. However, many small rivers drain into the sea along the Sanriku coast and the movement space of salmon is open directly to the ocean. To detect slight traces of their natal river in this area, homing individuals may have to survey the water mass properly. This evidence suggests that the complexity and extent of dilution could be the main factor causing chum salmon in the Sanriku coast to make restless vertical movements. Some deep dives could also have a significant role, not only to regulate the thermal condition but also to gain positional information by surveying several layers of the water column (Døving et al., 1985).

In conclusion, our results indicate that the risk of deterioration of body condition in the warm surface water triggered deep diving, but the traces of river water made salmon venture to return to the surface. Tolerance against rapid thermal change could enable salmon to use cool refuge in the bottom water. Salmon adjusted their behavioural strategy with the hydrographic structure of the sea to achieve

a balance between acquisition of directional cues and saving energy. As a result of such trade-offs, chum salmon generally prefer surface water, but make a series of remarkably deep dives. Changes in the environment such as temperature elevation could have a major effect on the balance of this trade-off. To address the question of how the physiological condition of individuals affects decision making, further studies will be needed.

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