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Swimming speeds and buoyancy compensation of migrating adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger

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Summary

Although the homing migration of Pacific salmon is well documented, the swimming behaviour of the returning salmon has been poorly described, principally as a result of the difficulties encountered in monitoring salmon behaviour in the sea. The present study describes the use of a recently developed electronic data logger to obtain simultaneous recordings of the swimming speed, depth, fin-beating activity and body angle of free-ranging chum salmon *Oncorhynchus keta* during their homing migration in coastal waters. Chum salmon migrated horizontally at speeds of 1.5–3.0 km h^{-1}. The gross horizontal distance salmon moved during total recording periods were 1.24- to 19.0-fold greater than the net distance from the release site to the retrieval points. It is suggested that homing salmon did not drift passively but swam actively to the spawning grounds. Salmon preferred the surface water, but also made frequent vertical migrations. The travelled depth of each salmon ranged from 0.36 to 0.64 km per hour. Salmon descended at faster rates and steeper angles than they ascended. Both tailbeat frequency and tail thrust were higher during the ascent than the descent phase. These results suggest that chum salmon spent more energy during the ascent than the descent phase. Profiles of descent rate assumed an arched shape with respect to a change in hydrostatic pressure, while ascent rate increased with decreasing depth. High tailbeat frequencies were found during the course of ascent, which suggests that the salmon did not regulate the volume of air in the swim bladder during short-term vertical migrations.

Key words: swimming speed, tailbeat frequency, angle, vertical rate, vertical migration, chum salmon, *Oncorhynchus keta*, homing migration, data logger.

Introduction

During their homing migration, Pacific salmon (*Oncorhynchus* spp.) move from their oceanic feeding grounds, through coastal waters, before entering their home rivers to spawn. Although numerous studies have described the general movements of Pacific salmon during their return migration, little work has been carried out on the swimming behaviour of the fish during this period. Where studies have been carried out, the results have suggested that the speed of migration is generally slower during their movement through the coastal zone than during the oceanic phase (Hansen et al., 1993; Quinn and Groot, 1984). There are two possible reasons for this change in migratory behaviour. First, the mechanisms controlling navigation are different in coastal waters and become more precise, with the salmon beginning to orientate with respect to hydrographic features (Hansen et al., 1993; Hasler et al., 1978; Quinn et al., 1989). Second, the coastal and estuarine zones may be the regions where anadromous fish need to remain for periods while they undergo the physiological adjustments that are required before the transition to fresh water and the beginning of the in-river spawning migration (Osanai et al., 1972; Quinn et al., 1989).

Previous studies have indicated that maturing sockeye salmon *Oncorhynchus nerka* seem to swim at speeds of approximately 50 cm s^{-1} in coastal waters (Quinn, 1988b) and migrate at an average ground speed of 46–59 cm s^{-1}, i.e. the net sum of swimming speed and water current speed around the fish (Madison, 1972). However, these swimming speeds were obtained using tagging and ultrasonic tracking techniques, and were either only estimates of the salmons' ground speed or biased by the speed of the tracking research vessel. Therefore, the actual swimming speeds of migrating Pacific salmon have not been measured directly.

Several other studies have demonstrated that Pacific salmon usually prefer the surface water during their homing migration but also undertake a number of active vertical migrations (Døving et al., 1985; Quinn et al., 1989; Ruggerone et al., 1990; Tanaka et al., 2000). The vertical migrations of some teleosts are suggested to be limited by the pressure difference between the minimum and maximum depth of the fish. Bloater

(*Coregonus hoyi*) in the Great Lakes do not migrate to the surface water, so that the pressure change for bloater during vertical migrations is less than 60 % (TeWinkel and Fleischer, 1998). However, homing chum salmon perform repeated vertical movements in shallow water to obtain directional cues (Døving et al., 1985) and also dive to depths in excess of 100 m for behavioural thermoregulation (Tanaka et al., 2000). Such large pressure changes and frequencies of vertical movements raise questions about the energetic cost of locomotion.

Vertical migration is a widely observed phenomenon in many teleost fishes including salmonids (Bevelhimer and Adams, 1993; Biette and Green, 1980; Brett, 1971; Clark and Levy, 1988). The adaptive fitness of migratory individuals should be increased if the cost of vertical movement is low (Gliwicz, 1986; Swift, 1976). However, there is so much uncertainty in the published data on fish that it is difficult to draw any firm conclusions regarding the energetic aspects of vertical migration (Alexander, 1972).

The chum salmon is a typical physostome, with a connection between the swim bladder and the gut. Physostome fish are able to fill their swim bladder by gulping air and venting it through the connecting duct (Brawn, 1962, 1969). Some authors have assumed that this unique function of the swim bladder allows physostome fish to make rapid, large vertical movements (Blaxter, 1985). However, it has also been suggested that, if a fish were to gulp air at the surface to give itself neutral buoyancy at depth, it would become grossly over-buoyant and unable to descend (Alexander, 1972; Ona, 1990). In addition, it has also been argued that physostome fish cannot secrete gas into the swim bladder at the rate required to aid buoyancy (Alexander, 1972; Wittenberg, 1958).

One method that can be used to investigate the energetic aspects of vertical locomotion and the role of changes in hydrostatic pressure is to study the fine-scale movements and swimming behaviour of fish as they undergo vertical migrations. The use of data loggers makes it possible to study a variety of behavioural variables (such as swimming depth and speed) of free-ranging aquatic animals. The use of data loggers was pioneered on seals, and the recent reduction in the size of the data loggers has led to a proliferation of studies on smaller aquatic mammals and seabirds (Kooyman et al., 1992; Naito et al., 1989; Wilson and Wilson, 1995). New developments, such as data loggers with an acceleration sensor, now permit studies that monitor the body motion of aquatic animals, such as the porpoising behaviour of free-ranging penguins (Yoda et al., 1999, 2001). In laboratory studies, the swimming patterns or tail thrusts of fishes have been monitored using a body accelerometer connected to a conductor cable (DuBois et al., 1976; DuBois and Ogilvy, 1978; Freadman, 1981). However, this method is limited to fish that will swim carrying wires, so the body angles or tailbeat activities of free-ranging marine fish have been little studied. The present study describes the use of a recently developed data logger to record simultaneously the swimming speed, depth, tailbeat activity and body angle of chum salmon during their homing migrations in coastal waters. The results of the study are discussed with respect to the behaviour of the salmon during vertical migration and in relation to buoyancy compensation.

Materials and methods

The methods and procedures used during the field experiments have been described previously (Tanaka et al., 1998, 2000). During October 1997 and 1999, 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). Salmon that return to this area of the coast ascend their natal rivers within a few weeks. During this period, the stomach of the fish is empty, suggesting that the salmon have already stopped feeding in preparation for the spawning migration.

The salmon were caught using a trap net in Otsuchi Bay and transferred to outdoor tanks at the Otsuchi Marine Research Center, Ocean Research Institute, the University of Tokyo. In total, 13 salmon were tagged with loggers and released. Individual fish were lightly anaesthetized using 2-phenoxyethanol, and total length and body mass were measured. 2-Phenoxyethanol has been shown to have no adverse effect on the homing behaviour of Pacific salmon (Quinn, 1988a). A data logger was sutured to the left side of

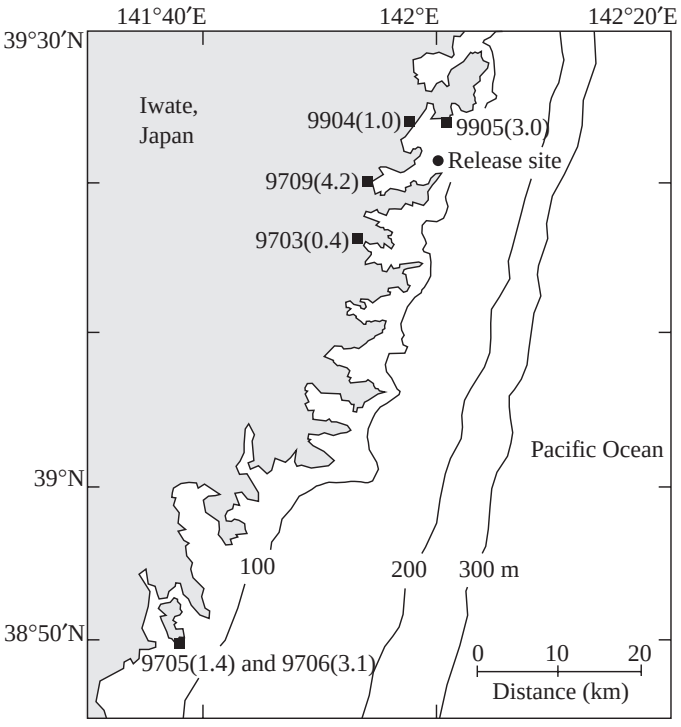

Fig. 1. Study site was off the Sanriku coast, Japan, in October 1997 and October 1999. Homing adult chum salmon were fished and released with loggers at the mouth of Otsuchi Bay. Filled squares indicate the sites where salmon were recovered. Unfortunately, the retrieval location of salmon 9902 was unknown. Numbers indicate salmon identification number, and numbers in parentheses correspond to the number of days before salmon were recovered. Lines show 100, 200 and 300 m contours.

the body, below the front edge of the dorsal fin, using nylon ties. The attachment procedures usually took less than 1 min. Each fish was transferred to a recovery tank and allowed 2–12 h to recover from anaesthesia and surgery. We observed the behaviour of chum salmon with loggers in a swim tank before release. After recovering from anaesthesia, the salmon with loggers were observed to behave (swimming, courtship, territorial defence behaviour, etc.) in a manner similar to intact individuals. After this recovery period, the fish were transferred to the mouth of the bay, a journey that took 15 min from the Institute, and released.

Two types of micro data logger (Little Leonardo Co. Ltd, Tokyo) were used on the chum salmon. In 1997, swimming speed and depth were monitored using a speed/depth/temperature (PDT) logger (UWE-200PDT; 42 g in air, 13 g in water, 20 mm in diameter, 90 mm in length, sampling frequency 1 Hz). In 1999, acceleration (sampling frequency 16 Hz) was also recorded together with the above variables using a speed/depth/acceleration/temperature (PD2GT) logger (W-190L-PD2GT; 60 g in air, 22 g in water, 21 mm in diameter, 117 mm in length). Both types of logger were cylindrical and had 1.0 megabyte (PDT) or 4.0 megabyte (PD2GT) of flash memory. Depth resolution was 0.05 m, and the maximum depth that could be measured was 190 m. The speed sensor of the loggers consisted of a propeller rotation counter. The stall speed of the recorder was determined experimentally to be 0.3 m s^{-1} for both loggers. Speeds below these values were considered indistinguishable from zero. To calibrate the speed sensor, we examined the relationship between propeller speed (rev s^{-1}) and the flow speed in a pool. The relationship was linear from 0.3 to 1.2 m s^{-1} for the PDT logger and from 0.3 to 0.9 m s^{-1} for the PD2GT logger, and the coefficient of determination (r) for both loggers was greater than 0.92.

The PD2GT logger was equipped with two piezo-resistive accelerometers (3G sensors; Akebono Brake Co. Ltd, Tokyo). The measuring ranges of the devices were −4 to 4$\boldsymbol{g}$ ($\boldsymbol{g}$=0.98 m s^{-2}). The PD2GT logger was attached to the salmon to record acceleration in two directions: the surging acceleration along the longitudinal body axis of the salmon and the swaying acceleration transversely across the salmon's body from right to left (Fig. 2). These recordings were used to detect the tail beat and body angle of chum salmon as described below.

Tail beat

To define the swaying acceleration profile with respect to the tail beat of salmon, the tailbeating activity of chum salmon was monitored by a video camera in the swim chamber simultaneously using PD2GT loggers. Although a number of salmon were studied, most fish, either with or without loggers, showed only casual swimming and resisted water flow with the caudal fin touching the wall of the chamber. Therefore, data were obtained from only a single fish (fork length 60.0 cm) that kept swimming actively at 50–70 cm s^{-1}. During steady swimming, there were sharp, distinct peaks of swaying

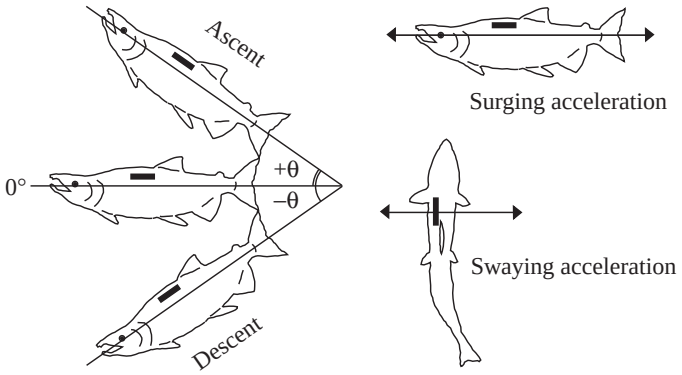

Fig. 2. Schematic diagram showing the direction of surging and swaying accelerations recorded by a data logger placed on the left side of the body of a salmon, below the front edge of the dorsal fin (black bar). Data for surging acceleration were converted to body angles, as described in the text. Body angles while salmon were ascending are presented as positive values, and body angles while salmon were descending are presented as negative values. θ, angle of ascent/descent.

acceleration, of which the amplitudes were greater than 1.0 m s^{-2} and frequencies were approximately 2.0 Hz (Fig. 3). Each of these peaks was confirmed as corresponding to one tail beat. When the salmon floundered, dashed or jumped, we could find no clear relationships between acceleration data and tailbeat frequencies because of offbeat, strong acceleration signals. When the salmon was drifting or resting, the amplitudes of the acceleration were relatively stable, but showed indistinct, small peaks because fish with swim bladders make continuous fin beats even in apparently still water (Webb and Weihs, 1994). However, we could not count tailbeat frequencies using the video camera or peaks of acceleration. We therefore counted tailbeat frequencies from acceleration data only while the salmon swam steadily. We defined distinct peaks of swaying acceleration as having amplitudes greater than 1.0 m s^{-2} and bottom–peak–bottom durations shorter than 1 s and used these criteria for measuring tail beats (Fig. 3). We also recorded the amplitudes of peaks as an indication of a tail thrust.

Body angle

The acceleration sensor along the longitudinal body axis measured the accelerations with respect to changes both in the movements of salmon and in gravitational acceleration (Fig. 2). Therefore, the amplitude of acceleration data when the salmon is still represents the gravitational acceleration component, which changes in response to the body angle of the salmon in the horizontal plane. This enabled us to determine the body angle of the salmon. To remove the acceleration of the movement, acceleration data were filtered by a lowpass filter (IFDL Version 3.1; WaveMatrics, Inc., USA). The lowpass filter characteristics for chum salmon are less than 0.8 Hz, which seems to be sufficiently low to remove tailbeat frequencies. The acceleration data along the longitudinal body axis were then converted to sine values and

to degrees. To re-adjust the horizontal level, we corrected the values of body angle recorded in a holding tank to 0°. We converted these 16 Hz sampling data to mean values for periods of 1 s. We describe body angles while the salmon is ascending as positive values and those while it is descending as negative values (Fig. 2). At low swimming speeds, both neutrally and negatively buoyant fish show 'tilting', with the body axis subtending an angle to the axis of progression (Webb, 1993). We therefore excluded data simultaneously recorded with a lower speed than the threshold of the speed sensor ($0.30\,m\,s^{-1}\approx0.5$ fork lengths s^{-1}) from our analysis.

After the retrieval of the loggers from the field experiments, the data were downloaded to a computer and analyzed using Igor Pro software (version 3.16J; WaveMatrics, Inc., USA). The data were treated statistically using StatView software (version 5.0; SAS Institute Inc., USA). We present all values as means ± S.D., unless noted otherwise, and use $P<0.05$ to indicate statistically significant differences.

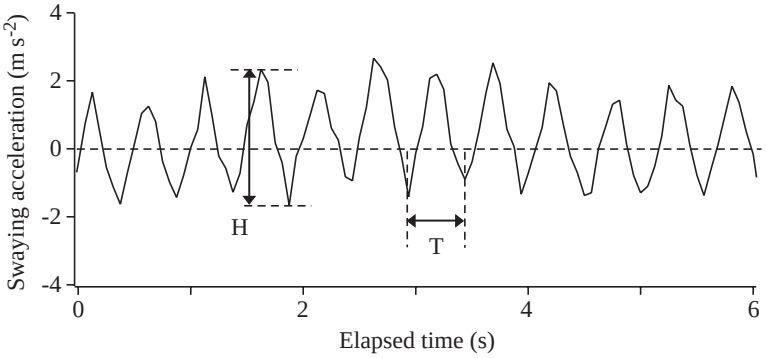

Fig. 3. A swaying acceleration profile of a chum salmon swimming at a flow rate of $0.7\,m\,s^{-1}$ in a chamber. Video recordings were used to confirm that each sharp peak in acceleration synchronized with one tail beat. When the salmon beat its caudal fin to the left, the acceleration reached a positive maximum value and *vice versa*. For the peaks indicated, the amplitude of the peak (H) was greater than $1.0\,m\,s^{-2}$, and bottom–peak–bottom duration (T) was less than 1 s. These values were recorded and converted to tailbeat frequency.

Fishermen on the Sanriku coast usually haul in their set nets twice a day and transfer salmon onto a boat. From the time/depth data recorded by the logger, we could easily determine when the salmon were transferred onto a boat. To exclude the data for salmon while in fishermen's nets, we omitted from our analysis any data recorded after the previous net-hauling event. In addition, from the analysis, we excluded data collected in the first hour after their release, which we believe is enough for the fish to flee from the researcher's vessel. We have already presented detailed characteristics of swimming depth and ambient temperature for the individuals studied in 1997 in a previous paper (Tanaka et al., 2000).

Results

General behaviour of the salmon

The salmon release sites and recovery locations are shown in Fig. 1. Two fish were recovered in trap-nets set in river mouths, while the others were caught either by trap-nets or by gill-nets in the sea. One logger was retrieved from a fish market, but the recovery site of the fish was unknown (salmon 9902). In 1997, the swimming depths and speeds were recorded from four chum salmon. In 1999, three PD2G loggers were recovered, but the acceleration sensor on one data logger had not been functioning. Therefore, data on swimming depths and speeds were obtained from seven fish, from which two provided information on tailbeating activity and body angle, which were recorded simultaneously. In 1997, data were recorded from the time of release to the retrieval of the loggers. However, in 1999, because of the life of the battery, the loggers stopped recording prior to the retrieval date. Recording periods ranged from 0.36 to 4.11 days.

Table 1 summarizes the data on the swimming depth and swimming speed recorded from each of the tagged salmon. The salmon made frequent dives from the surface water, including a number of extended deep dives. However, deep dives were recorded less frequently around midnight. An example of

Table 1. *Sex, length, mass, recording periods and summary statistics for behavioural variables of homing chum salmon*

Salmon no.	Sex	Fork length (cm)	Body mass (g)	Recording period (days)	Swimming depth (m)	Horizontal distance moved per hour (m)	Mode range of swimming speed ($m\,s^{-1}$)
9703	M	68.5	3750	0.36	76.0±47.1	2416.8	0.9–1.0
9705	M	67.5	3440	1.38	90.1±41.5	2503.0	0.5–0.6
9706	M	70.5	3920	3.01	107.8±44.3	3036.7	0.6–0.7
9709	M	65.0	3080	4.11	55.5±44.4	1507.2	<0.3
9902	M	65.0	3700	1.33	103.7±51.0	2579.5	0.8–0.9
9904	F	62.0	3042	0.86	11.0±15.5	1791.6	0.7–0.8
9905	F	58.0	2460	1.59	88.7±42.9	2315.8	0.6–0.7

Sampling frequency was 1 Hz for depth and speed.
Values of swimming depth are mean ± S.D. (N=75210–354621).

the typical pattern of swimming behaviour of homing chum salmon is demonstrated by the data recorded from salmon 9904 (Fig. 4).

Typical frequency distributions of swimming speed for two salmon (salmon 9706 and 9709) are shown in Fig. 5. Mode swim speeds of each salmon ranged from 0.5–0.6 to 0.9–1.0 m s^{-1}, with the exception of salmon 9709, which often moved below the threshold of the speed sensor (Table 1). However, the distributions of swimming speeds showed a broad peak, suggesting that the salmon had a broad range of preferred speed of 0.5–1.0 m s^{-1}. Chum salmon rarely swam at speeds faster than 1.5 m s^{-1}. To describe diurnal pattern of swimming speed, we divided the speed data into midnight (21:00–03:00 h), morning (03:00–09:00 h), midday (09:00–15:00 h) and evening (15:00–21:00 h) periods. Swimming speeds tended to be lowest at midnight (0.34±0.36 to 0.77±0.25 m s^{-1}) and highest at midday (0.57±0.39 to 0.92±0.19 m s^{-1}) (Friedman's test, χ^2=10, P<0.05, N=7). However, we could find no clear relationships between swimming speed and tidal cycle. The horizontal distances that salmon migrated were derived from the swimming speeds and the rates of change of depth (vertical rate) by simple trigonometry. Chum salmon moved horizontally through coastal waters at swimming speeds of 1.5–3.0 km h^{-1} (i.e. 0.5–1.0 m s^{-1}; Table 1). In 1997, the ratio of gross horizontal distance to net horizontal distance, which was estimated from the positions of the release and retrieval sites, ranged from 1.2 to 3.2. The exception was salmon 9709, with a value of 19.0, which was recovered from the river mouth in Otsuchi Bay 4.2 days after release. The ratio was also calculated for salmon released in 1999. The values were 7.7 for salmon 9904 and 1.6 for salmon 9905. However, in these two salmon, data were not recorded throughout the whole period because of battery life.

The vertical distance traveled per hour by each salmon ranged from 0.36 to 0.64 km per hour. Salmon moved continuously from side to side throughout the recording periods, and the tailbeat frequencies were 1.80 Hz for salmon 9902 and 9904. In general, chum salmon maintained their body axis within an angle of ±40 ° with a modal range of –4 ° to +4 °. Typical frequency distributions of body angle for salmon 9904, which were recorded simultaneously with swimming speed data faster than 0.3 m s^{-1}, are shown in Fig. 6. The patterns of ascent angle (positive values) and descent angle (negative values) were not symmetrically distributed. The

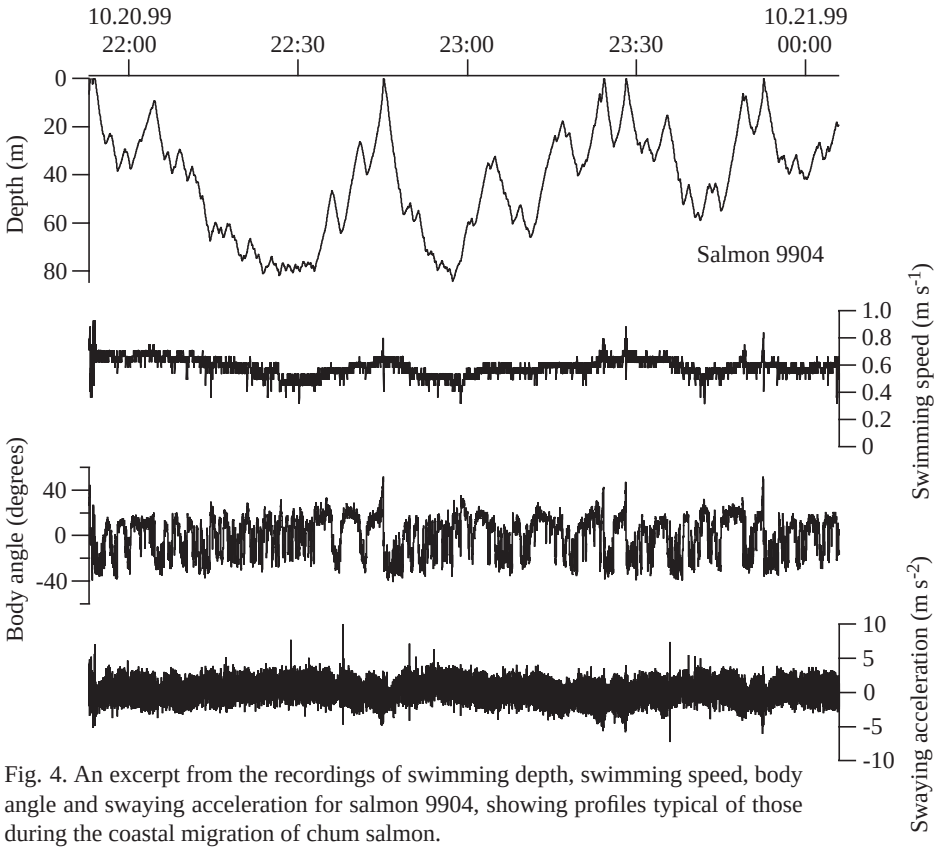

Fig. 4. An excerpt from the recordings of swimming depth, swimming speed, body angle and swaying acceleration for salmon 9904, showing profiles typical of those during the coastal migration of chum salmon.

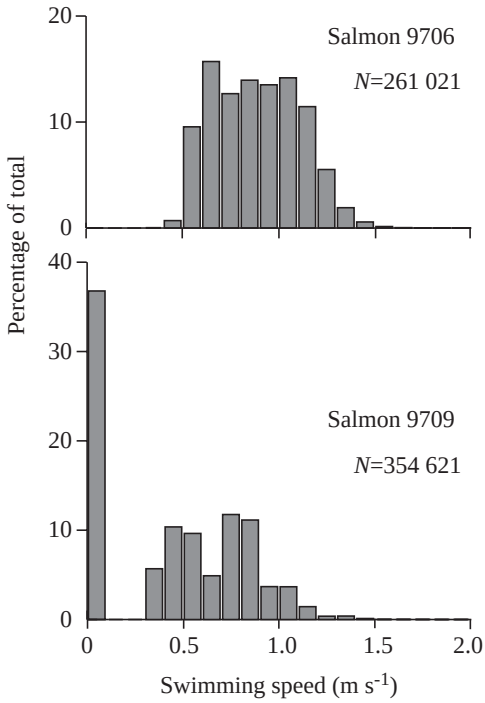

Fig. 5. Frequency distributions of swimming speeds for two homing chum salmon (salmon 9706 and 9709) for the entire recording period in October 1997. Salmon 9706 was recovered approximately 70 km away 3.1 days after release, and salmon 9709 was recovered approximately 7.9 km away 4.2 days after release.

negative side of the distribution assumed a slightly bimodal pattern, with a broad peak around –20 °, although the positive side was relatively smooth.

Comparison between the descent and the ascent phases

To facilitate analysis, data sets were chosen for which changes in depth during descents and ascents were greater than 10 m. The descent and ascent were not always paired, so the numbers of these are not equal. In total, 791 descents and 808 ascents were recorded, involving 206 descents and 209 ascents from two salmon whose accelerations were recorded simultaneously. Chum salmon undertook these vertical descents and ascents every 6.7–14.6 min.

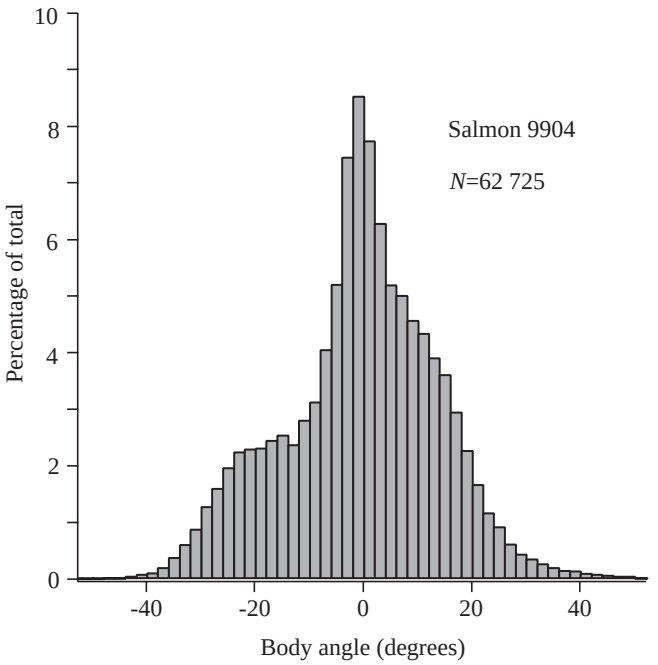

Fig. 6. Frequency distribution of body angles for a chum salmon (9904) recorded simultaneously with swimming speeds higher than 0.3 m s^{-1}. The mean body angle was 0.3±14.0 °; that for salmon 9902 was –0.6±14.8 ° (not shown) (means ± S.D., *N*=110 499).

Table 2 summarizes the duration, change in depth, vertical rate, swimming speed, tailbeat frequency, tailbeat frequency per 1 m depth change, amplitude of tail beat and body angle during the descents and ascents. There were significant differences in most of these behavioural variables between the descent and ascent phases (Mann–Whitney *U*-test). The change in depth during ascents (16.8±6.6 to 29.5±21.0 m) was significantly greater than for descents (14.6±5.5 to 30.4±23.8 m) only in salmon 9904. The vertical descent rates (0.26±0.07 to 0.37±0.11 m s^{-1}) were significantly faster, tailbeat frequencies per 1 m depth change (2.9±1.8 and 6.2±1.6) were significantly lower and amplitudes of tail thrust (3.0±1.2 to 2.5±0.6 m s^{-2}) were significantly smaller than during the ascent phase (0.22±0.07 to 0.29±0.11 m s^{-1}, 7.8±1.7 and 9.6±1.9 and 4.5±1.2 to 4.4±0.6 m s^{-2}). However, there were no significant differences in the swimming speeds between the descent (0.67±0.12 to 1.04±0.15 m s^{-1}) and ascent (0.66±0.43 to 1.03±0.19 m s^{-1}) phases. Consequently, salmon swam at a significantly steeper angle during the descent (–25.3±5.3 ° and –22.9±4.2 °) than the ascent (19.7±7.2 ° and 18.3±3.8 °) phase. These results indicate that the salmon must have taken a shorter time to move to a given depth during a descent than during an ascent. In fact, the durations of descents (51.8±18.9 to 89.3±48.1 s) were significantly shorter than the durations of ascents (71.1±35.5 to 113.1±63.1 s) for six of the seven individuals.

Chum salmon showed frequent vertical movements and

Table 2. *Summary statistics for vertical movements greater than 10 m of homing chum salmon*

Salmon no.		*N*	Duration (s)	Change in depth (m)	Vertical rate (m s^{-1})	Swimming speed (m s^{-1})	Tailbeat frequency (Hz)	Tailbeat frequency per 1 m depth change	Amplitude of tail thrust (m s^{-2})	Body angle (degrees)
9703	Descent	21	89.3±48.1	30.4±23.8	0.31±0.10‡	0.85±0.10				
	Ascent	29	91.3±55.8	23.7±20.3	0.25±0.07	0.83±0.13				
9705	Descent	117	72.3±38.5*	23.4±15.9	0.32±0.10‡	0.70±0.11*				
	Ascent	106	100.9±58.2	29.5±21.0	0.28±0.07	0.72±0.12				
9706	Descent	145	78.2±52.0‡	26.4±20.1	0.33±0.07*	1.04±0.15				
	Ascent	154	87.7±50.2	26.1±18.7	0.29±0.07	1.03±0.19				
9709	Descent	214	69.4±41.9*	20.2±14.7	0.30±0.07‡	0.55±0.28*				
	Ascent	217	75.1±42.5	19.4±13.6	0.29±0.07	0.66±0.43				
9902	Descent	148	54.2±22.7*	19.7±12.9	0.37±0.11*	0.72±0.15	1.1±0.8*	2.9±1.8*	3.0±1.2*	–25.3±5.3*
	Ascent	144	72.4±36.9	20.0±12.1	0.29±0.11	0.72±0.14	2.0±0.3	7.8±1.7	4.5±1.2	19.7±7.2
9904	Descent	58	51.8±18.9*	14.6±5.5‡	0.29±0.07‡	0.69±0.10	1.8±0.4*	6.2±1.6*	2.5±0.6*	–22.9±4.2*
	Ascent	65	71.1±35.5	16.8±6.6	0.25±0.06	0.70±0.09	2.3±0.2	9.6±1.9	4.4±0.6	18.3±3.8
9905	Descent	88	78.4±28.7*	20.7±10.7	0.26±0.07*	0.67±0.12				
	Ascent	93	113.1±63.1	24.9±17.7	0.22±0.07	0.68±0.07				

*Significantly different from the value for the ascent phase; *P<0.001, ‡P<0.05.
Values are mean ± S.D.

sometimes dived from the surface to a depth of over 100 m. The vertical movements of salmon appear not to be independent of the changes in hydrostatic pressure acting upon the swim bladder and body cavity, which in turn change the total buoyancy of the salmon. To describe the changes in behavioural variables (vertical rate, speed, body angle and tailbeat frequency per 1 m depth change), we chose descents from the surface (≤5 m) and ascents to the surface for which the depth changes were greater than 25 m. To illustrate the changes over the course of descents and ascents, each mean value was calculated while the salmon passed through the initial, middle and final 5 m depth ranges of vertical travel. Fig. 7 shows the results for two salmon (9902 and 9904) as typical examples of changes in behavioural variables as a function of changes in hydrostatic pressure.

Except for swimming speed, which was maintained at approximately 0.8 m s^{-1} in both the descent and ascent phases, the behavioural variables changed significantly with respect to the change in depth (Friedman's test; nine descents and 13 ascents). Salmon initiated descent movements at an angle of approximately −24 ° and reached the steepest angle (approximately −38 °) during the middle of the dive; the angle then decreased again to approximately −23 °. Ascent angles were lowest at the beginning of the ascent and then increased; however, ascent angles were always less than 30 °. Vertical descent rates tended to vary directly with body angle and were fastest during the middle of the descent. Vertical ascent rates increased with decreasing depth. Tailbeat frequencies per 1 m depth change tended to change inversely with vertical rate. In both the descent and ascent phases, tailbeat frequencies were highest at the beginning of the vertical migration, and for comparable phases of vertical movement tailbeat frequencies were greater during ascent than during descent. However, there was no significant difference between tailbeat frequencies in the final phase of ascents and those in the initial phase of descents (Mann–Whitney *U*-test, *U*=36.0, not significant, *N*=9).

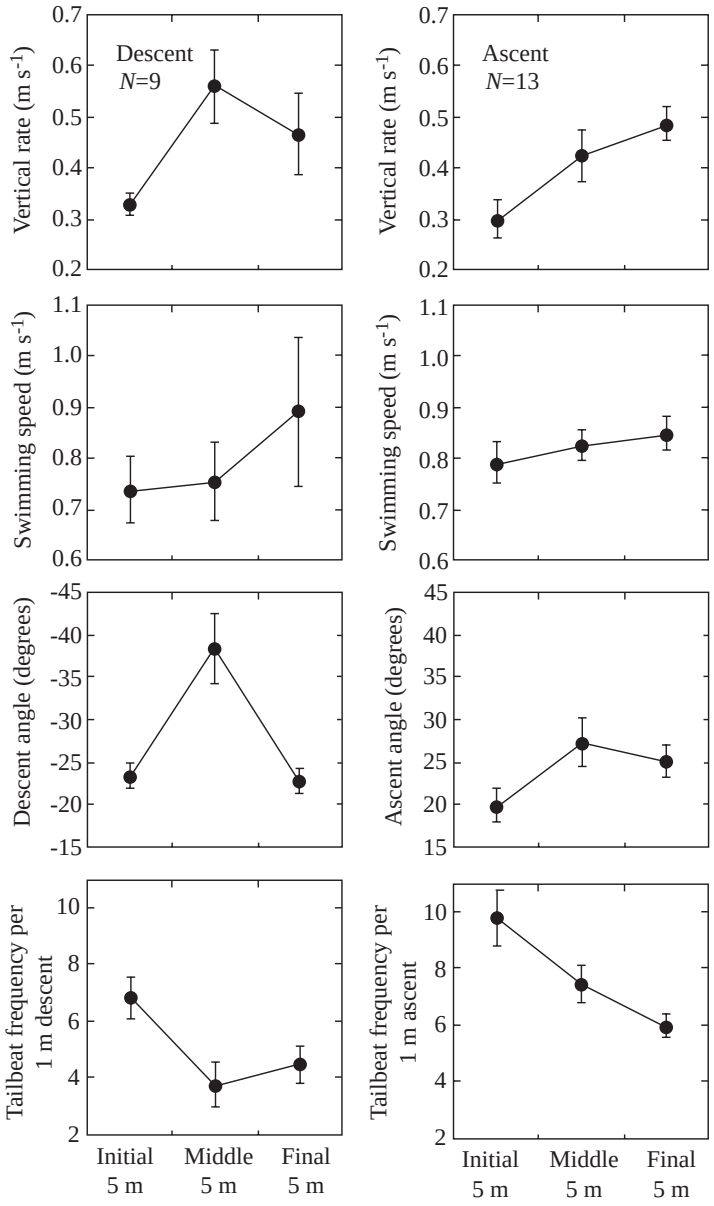

Fig. 7. Mean values of vertical rate, swimming speed, body angle and tailbeat frequency per 1 m depth change for the initial, middle and final 5 m ranges of vertical movements whose total change of depth was greater than 25 m for salmon 9902 and 9904. Values are means ± S.E.M. The left panels shows descents (*N*=9) that started from the surface water (≤5 m deep) and the right panel shows ascents (*N*=13) that finished in the surface water. Apart from swimming speed, all behavioural variables changed significantly with respect to the change in the range of vertical travel (Friedman's test).

Discussion

Before discussing the results, we should briefly comment on the effects of logger attachment on the behaviour of homing individuals. Mellas and Haynes (1985) conducted experiments to determine the effects of various tag attachments on the swimming behaviour of rainbow trout and suggested that stomach tagging is the best method of transmitter attachment. Because our data logger included a swimming speed sensor, we had to use external attachment. However, we observed the behaviour of chum salmon with loggers in swim tanks and could find no clear differences in behaviour from that of intact individuals. In our preliminary study, we transferred mature chum salmon that had been caught in the river mouth before experiments to the same release point as in our present study and found that they had returned to the river mouth after several hours (H.T., Y.T. and Y.N., unpublished data). It is therefore likely that the salmon fitted with our logger retain their homing motivation and maintain horizontal movement.

Some authors have related deep dives of salmon to abnormal behaviour caused by sensory ablation. For example, Døving et al. (1985) and Yano and Nakamura (1992) found

that anosmic salmon made prolonged dives to the sea bottom with very little net horizontal progression. However, the behaviour of fish can vary greatly among species and environmental conditions. We have not observed such deep dives immediately after release (Tanaka et al., 1998, 2000). The series of deep dives found in our studies resulted from behavioural thermoregulation, not from stress caused by our methods (Tanaka et al., 2000). We recorded the swimming behaviour of some chum salmon for more than a week, but could find no clear differences between the earlier and later parts of this period (Tanaka et al., 2000). The present results showed that tagged chum salmon showed a diurnal pattern during recording periods. Mode range of swimming speeds of chum salmon in our results was 0.74–1.31 fork length s^{-1}, which includes both the predicted optimal speed that minimizes the cost of locomotion (Brett, 1995; Weihs, 1973b) and the estimated horizontal speed of migrating Pacific salmon (Quinn, 1988b). Recorded vertical rates are also similar to those in previous studies on chum salmon in the sea (Soeda et al., 1985; Yano and Nakamura, 1992). Thus, we believe that our results provide reliable data for the swimming behaviour of homing chum salmon under natural conditions.

Our results indicate that salmon do not migrate immediately into their home rivers to spawn, but undertake extensive vertical and horizontal movements within the sea. Differences in geography, hydrographic features, physical condition or reproductive strategy could force salmon to make such detours during their migration in coastal waters. The estimated ratio of gross horizontal distance to net horizontal distance, which was greater than 1.0 for all fish, indicates that homing salmon did not drift passively with current flow but swam actively during the study periods. The high ratios for some fish suggested that coastal migrations are not strongly oriented but contain an element of random movement. In the data for salmon 9709, which was recovered in the river mouth near the release site, we found both a high ratio of gross to net movement and swimming speeds that were slower than the threshold of the speed sensor. This suggests that the swimming speeds of homing salmon change depending upon the geographic position of the fish within the sea. We found no clear relationships between swimming speed and tidal cycle. However, in addition to swimming speed, positional information about the individuals and the speed of the water currents through which they swim are required for a precise interpretation of the data. Future studies using both data loggers and positioning techniques will be required to address this question.

If salmon could achieve neutral buoyancy throughout their vertical movement, the depth profiles of descents and ascents should be symmetrical, and there would be no difference in energetic cost between them. However, as shown in Fig. 7, the profiles of descents and ascents were clearly asymmetrical. Chum salmon therefore appear to be unable to maintain neutral buoyancy during vertical movements. Could salmon achieve neutral buoyancy at the bottom of their descents? There are two possible methods of adding gas to the swim bladder: (i) air- or bubble-gulping at the surface and (ii) gas secretion during the bottom phase (Alexander, 1972, 1993; Brawn, 1962). If a salmon filled its bladder before a descent to achieve neutral buoyancy at its final deep destination, a descending salmon would have to deal with drag and buoyancy factors operating in the opposite direction to their movement. But, the ascent of the salmon could be assisted by its buoyancy, thus reducing energetic costs. In fact, some diving animals and seabirds are over-buoyant at the surface at the beginning of a dive because of air-filled lungs (Minamikawa et al., 2000). Thus, during the ascent phase, they have been observed to stop swimming because their buoyancy provides sufficient propulsive power for ascent as hydrostatic pressure decreases (Williams et al., 2000). However, if a salmon were to secrete gas into its swim bladder during the bottom phase, this would make it neutrally buoyant and provide it with sufficient uplift during the ascent phase without requiring extra propulsive power at the beginning of the descent.

However, the results of the present study do not support either of these proposals. Our results indicate that the tailbeat activity of chum salmon was continuous during the ascent phase. The tailbeat frequency per unit depth change decreased during the ascent and was higher during comparable parts of vertical migration than during the descent. Moreover, tail thrust during the ascent phase was greater than that during the descent phase. These data indicate that the salmon used more energy during the ascent, although ascent rate was slower than descent rate, and that chum salmon had a volume of air in the swim bladder great enough to achieve neutral buoyancy only in the surface water and, as a consequence, that they were negatively buoyant throughout the vertical movement. It seems that chum salmon do not increase their buoyancy prior to a dive. Wittenberg (1958) reported that the replacment of the gas volume of the emptied swim bladder of captive rainbow trout was 30–55 % complete at 7 days and 32–100 % complete at 13 days. This suggests that, if a fish of neutral buoyancy in the surface water dived from the surface to a depth of 10 m, it would take 7 days or more to recover its neutral buoyancy by gas secretion. Thus, we cannot reject the possibility that additional gas was secreted into the swim bladder, but the volume would have been very small for vertical migrations that occurred approximately every 6–15 min, as observed in the present study. Some authors have reported that descent rates were faster than ascent rates in the physostomes (Blaxter, 1985). The functional reasons have not been discussed fully, but could have the same causes as in the present study.

It is not so clear why chum salmon, which are typical physostomes, have not evolved a rapid regulation of the swim bladder to save energy during vertical movements. Many studies on Pacific salmon indicate that chum salmon spend most of their life in the surface water (Ogura and Ishida, 1995). Thus, the function of a swim bladder in salmon is probably related to acquiring neutral buoyancy in the surface water, rather than modulating buoyancy for changing depth. In coastal

waters, homing salmon dive to depths of over 100 m for behavioural thermoregulation (Tanaka et al., 2000). In such cases, salmon could save metabolic energy costs in cool thermal refuges, where they often remain submerged for periods in excess of 24 h. Possibly, the benefit of thermoregulation can outweigh locomotor costs caused by the added negative buoyancy at depth if dive duration is long enough.

However, even if salmon cannot rely on the swim bladder for rapid vertical migration, the pneumatic duct of the swim bladder could still play a significant role during extended dives. For example, if gas were lost accidentally or through a duct of the swim bladder, the salmon could recover neutral buoyancy at the surface quickly by gulping air. Our results indicated that tailbeating activity was highest during the initial phase of a dive, suggesting that salmon cannot be negatively buoyant at the water surface. To maintain neutral buoyancy, the volume of the swim bladder needs to be approximately 5 % of the fish's volume in salt water (Alexander, 1993; Schmidt-Nielsen, 1990). The typical specific gravity of a fish without a swim bladder is 1.07, so a chum salmon of average body mass in the present study (3.3 kg) without a logger could achieve neutral buoyancy at the surface with an air volume of 156 ml in the swim bladder. An additional 9.8 and 18.0 ml of air would be needed to balance with the PDT and PD2GT logger, respectively.

Our data show that negative buoyancy could make salmon descend passively with a lower energetic cost of locomotion than during the ascent phase. This finding suggests that the salmon could descend by gliding to some extent. In addition, the descent angle and vertical rate of descent of chum salmon tended to be greatest in the middle of the descent, not during the final phase. Decreases in descent rates are usually observed when aquatic animals utilize negative buoyancy for gliding movements (Weihs, 1973a; Williams et al., 2000). During vertical movements, these animals show three phases of movements: steady stroking, stroke-and-glide swimming and a gliding phase (Williams et al., 2000). The gliding phase is characterized by a marked and prolonged period during which no locomotor movements occur. In the present study, we found no prolonged interruption of tailbeat activity during descents. Therefore, our results suggest that descending salmon could 'swim-and-glide', but could not switch to a gliding phase. It is likely that the body form, small pectoral fin and composition of chum salmon did not allow them to utilize downforces effectively and to adopt a gliding strategy during the descent phase. We believe that the data loggers did not affect the buoyancy regulation of salmon, although the weight of the loggers could have contributed somewhat to swim-and-gliding during descent and the extra work during ascent. Neutrally buoyant loggers will be required in further studies.

That the steepest body angle is found during the middle phase also suggests that salmon actively manoeuvred themselves during the descent phase. It appears that descending chum salmon would not be able to prevent an uncontrolled descent unless they had readapted prior to the dive. In coastal waters during the homing migration, the functional significance of the vertical movement of Pacific salmon has been linked with navigation (Døving et al., 1985; Quinn et al., 1989; Ruggerone et al., 1990) and thermoregulation (Tanaka et al., 2000). In both cases, the depths of homing chum salmon were related to the fine-scale hydrographic features in the sea. These precise and regular behavioural patterns suggest that salmon did not select a swimming depth at random. It appears that chum salmon anticipate the required depth of a dive and subsequently regulate their descent rate.

If a salmon were to maintain its body angle at a given value, the change in vertical rate would directly reflect the change in swimming speed. However, our data indicate that the body angle of salmon changed with vertical rate (Fig. 7). As a result, swimming speed was relatively stable during vertical movements (Table 2). This constant swimming speed, which was unexpected, raises a question regarding its adaptive significance. One possible explanation could be a stabilizing function as a result of continuous swimming at a particular speed. Fish with swim bladders can be close to hydrostatic equilibrium, but any disturbance will be destabilizing. This could explain the continuous fin beating of fish in apparently still water (Webb and Weihs, 1994). Therefore, it is possible that salmon have to swim at a particular speed to stabilize themselves during the descent and ascent phases. Alternatively, it is possible that the salmon maintain an optimal swimming speed that would minimize locomotor energetic cost. Hinch and Rand (1998) reported that the tailbeat frequency of upriver-migrating sockeye salmon varied little within the different reaches of the river. These authors suggested that sockeye salmon have an optimal swimming speed that could minimize energy use while migrating upstream. However, the constant speed during vertical migration cannot be explained by the previously developed optimal-speed model (Weihs, 1973b), which did not consider the effects of buoyancy forces. In future research, we need to consider not only the stabilizing function but also the correct model of an optimal swimming speed during vertical migration that incorporates changes in buoyancy for a better understanding of the swimming speeds of vertical movements.

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