Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags

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ABSTRACT

Eight temperature-recording data storage tags were recovered from three salmonids in Alaska (pink and coho salmon and steelhead trout) and five chum salmon in Japan after 21–117 days, containing the first long-term records of ambient temperature from Pacific salmonids migrating at sea. Temperature data imply diel patterns of descents to deeper, cooler water and ascents to the surface. Fish were found at higher average temperatures at night, with narrower temperature ranges and fewer descents than during the day. Fish tagged in the Gulf of Alaska were at higher temperatures on average (10–12°C) than chum salmon tagged in the Bering Sea (8–10°C). Chum salmon were also found at a wider range of temperatures (−1–22°C vs 5–15°C). This is probably related both to the different oceanographic regions through which the fish migrated, as well as species differences in thermal range and vertical movements. Proportions of time that individual fish spent at different temperatures seemed to vary among oceanographic regions. Steelhead trout may descend to moderate depths (50 m) and not be limited to the top few metres, as had been believed. Japanese chum salmon may seek deep, cold waters as they encounter warm surface temperatures on their homeward migrations. Temperature data from all fish showed an initial period (4–21 days) of day and night temperatures near those of sea surface temperatures, suggesting a period of recuperation from tagging trauma. A period of tagging recuperation suggests that vertical movement data from short-term ultrasonic telemetry studies may not represent normal behaviour of fish. The considerable diurnal and shorter-term variation in ambient temperatures suggests that offshore ocean distribution may be linked more to prey distribution and foraging than to sea surface temperatures.

Key words: Bering Sea, data storage tags, North Pacific, Pacific salmon, steelhead trout, tagging effects, thermal habitat

INTRODUCTION

Five species of Pacific salmon, sockeye (*Oncorhynchus nerka*), chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), and chinook (*O. tshawytscha*), and steelhead trout (*O. mykiss*) are found widely distributed across the North Pacific Ocean and in the Bering Sea, with a high degree of overlap in their overall ocean distributions, generally north of about 40°N-45°N latitude (Groot and Margolis, 1991). With the end of high-seas driftnet fishing in 1992, all legal fisheries have been restricted to the numerous coastal and freshwater fisheries that operate from California to Japan. The major salmon-producing countries of the North Pacific (Canada, Japan, Russia, and the United States) have for many years conducted open-ocean research on Pacific

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salmon and steelhead, with the aims of understanding distribution, overlap in stock ranges, relative abundance, migration routes, and growth.

While 50 years of ocean research has greatly advanced our understanding of the distribution and many aspects of the biology of Pacific salmonids, the behaviour and habitat use of individual salmon on the high seas remain poorly understood. Tagging studies have yielded general outlines of distribution and migration patterns (Ogura and Ito, 1994; Myers *et al.*, 1996), but our knowledge of the environment the salmon travel through is usually limited to the release and recovery locations. The long-term nature of compiling enough tag data to see a distribution pattern may conceal important environmental characteristics by combining data from years and seasons when conditions might have been substantially different. Vertical distribution has been inferred from use of various types of fishing gear (Manzer, 1964; Mishima *et al.*, 1966; Ueno, 1992) and hydroacoustics (Sakai *et al.*, 1997). These studies offer only glimpses of where salmon are at a single instant. Radio and ultrasonic tags have been used to follow adult salmon behaviour and habitat at sea, both on the high seas (Ogura and Ishida, 1992, 1995; Ogura, 1994) and in coastal waters (Madison *et al.*, 1972; Quinn *et al.*, 1989; Ruggerone *et al.*, 1990; Candy *et al.*, 1996). However, these tags require tracking by a vessel, and the signal is typically lost in a few days. Results of tagging studies are also clouded by the unknown effects of tagging itself. The expense of open-ocean research imposes numerous limits, and each technique is a tradeoff between the number of fish sampled and the amount of data that can be acquired from each fish.

More precise knowledge is needed of how salmon behave and where they are during the course of a day, a season, or an entire period of residence in the ocean. We need to understand how salmon respond to physical factors such as temperature, salinity, and currents, and to episodic events such as El Niño, to periodic shifts in climate patterns, and to pervasive changes such as global warming. In addition, temperature affects the metabolic rate of salmon, and precise knowledge of thermal habitat is required for accurate bioenergetic modelling of feeding and growth. Such knowledge is useful not only for understanding growth of individuals, but also for predicting effects of changes in abundance, such as hatchery augmentation or overharvesting, on overall biomass of populations. Beyond the utility of better understanding salmon life history and ecology, salmon and other marine organisms carrying archival or data storage tags can be agents for much more extensive sampling of ocean environments than is possible from oceanographic research vessels and other platforms.

Application of data storage tags to Pacific salmonids has been discussed and promoted in recent years as a means of better understanding how salmon utilize the ocean environment. The use of these tags has been considered at several recent meetings of the North Pacific Anadromous Fish Commission, and a workshop convened to evaluate application of acoustic and data storage tags to Pacific salmon made several recommendations on the next steps that should be taken to improve our knowledge of movement and habitat utilization (Boehlert, 1997). The first proposal was to use existing data storage tags in a high-seas tagging study to verify their utility. Our study addresses that recommendation. The relatively large size and expense of currently available data storage tags that record a wide suite of parameters (including light level for geolocation) led to recommendations for use of cheaper, reduced-parameter data storage tags to demonstrate their practicality in studies of adult salmon at sea (Myers, 1997). Environmental data recorded concomitantly during tracking with radio and ultrasonic tags can be correlated with knowledge of the fish's location and depth for the few days fish can be tracked, but it would be useful to have prolonged data records of environmental variables such as temperature and depth as encountered by individual fish.

Data storage tags have been successfully used on Atlantic salmon and sea trout (*Salmo salar* and *S. trutta*; Sturlaugsson, 1995; Karlsson *et al.*, 1996; Sturlaugsson and Gudbjornsson, 1997; Sturlaugsson and Thorisson, 1997), and on Pacific salmon in coastal waters around Japan (Ogura, 1997). Atlantic salmon in Iceland and the Baltic Sea were found to spend most of their time in the top three or four metres, with occasional dives to 30–110 m, while chum salmon near Japan stayed in deep water (100–210 m) during the day and in shallower water at night. The only earlier reported use of data storage tags on Pacific salmon in offshore waters has been the recovery of a depth-recording tag from a chum salmon migrating from the southern Kuril Islands to Hokkaido (Ishida *et al.*, 1998). This fish showed a clear pattern of daily vertical movement, remaining near the surface at night and making frequent round trips to 40–60 m during the day.

In 1998 two programmes succeeded in placing different types of data storage tags on salmonids in the North Pacific Ocean and Bering Sea. In one experiment, tags recording temperature, depth, and light were successfully implanted in 25 maturing chum salmon in the Bering Sea (Wada and Ueno, 1999).

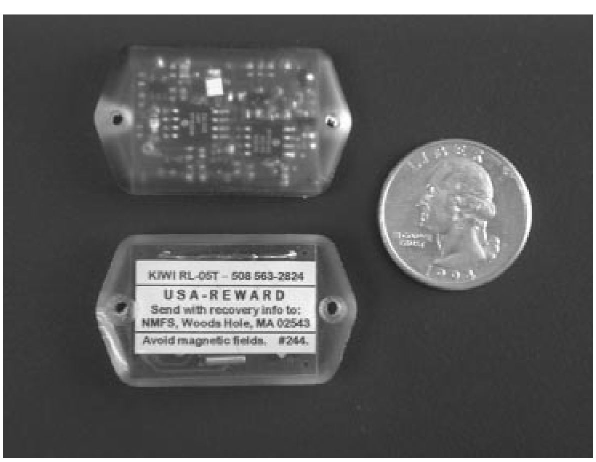
We report here the results of the other study, in which smaller tags, which recorded temperature only, were placed on Pacific salmon and steelhead trout during three research cruises. Recoveries of these tags provide the first records of temperature data recorded from maturing Pacific salmonids migrating at sea. We discuss patterns of diurnal behaviour implied by the temperature data, report the temperature ranges and proportions of time at different temperatures, and consider evidence of tagging trauma affecting the subsequent behaviour of the fish.

MATERIALS AND METHODS

Tags

The tags are small, microprocessor-based data loggers embedded in an environmentally resistant clear urethane with a return address label. They are a version of the Kiwi Ready Logger RL-05T (manufactured by Conservation Devices, Inc.; use of brand name does not imply endorsement by National Marine Fisheries Service). They weigh ≈9.5 g (3.3 g in water) and measure 40 × 23 × 8 mm, with two holes, one at each end of the long axis (Fig. 1). They measure temperature over a range of −5°C to 30°C with an accuracy of ±0.2°C, are functional to over 1000 m depth, and have an endurance (battery life) of more than three years. There is sufficient memory to hold 8192 observations. The memory is initially filled at a rate of one observation per 14.0625 s. After the memory is full, half the old data are released (every other value) and new data are collected at half the previous collection rate (new interval of 28.125 s), thereby automatically optimizing the temporal resolution for the total time over which the tag is deployed. This process repeats each time the memory is full; in our experiment we recovered tags with observations collected at 7.5, 15, and 30 minute time intervals. Data collection is continuous from time of manufacture, and was re-initiated to the shortest sampling interval by activating a magnetic reed switch in the tag shortly before tag application. On recovery, data were downloaded to a computer with a reader that receives infrared signals from a light-emitting diode in the tag. Tags were calibrated at manufacture and tested again after recovery. Known temperature events, such as sea surface temperatures (SST) at release locations and thermal signals induced after recovery, were correlated with temperature and time recorded by the tag.

Figure 1. Temperature-recording data storage tag used on Pacific salmonids in 1998. Diameter of coin is 24 mm.



Fish capture and tagging

Fish were caught for tagging during salmon research cruises aboard three vessels in 1998. On two cruises, fish were caught by surface longline baited with salted anchovies; on the other cruise, they were caught by a midwater rope trawl towed at the surface at 2.6 m s^{-1}. Trawl-caught fish were tagged at 51°34′N and 50°35′N on 164°W longitude on 3 May 1998 and at 44°37′N, 145°00′W on 19 May 1998. Along 180° longitude, tagging was conducted at evening longline stations (one hour soak time) between 45°N and 58°30′N in the North Pacific and Bering Sea between 25 June and 15 July 1998. Fish caught in morning longline sets (two hour soak time) were tagged at 48°50′N, 165°W on 27 June 1998 and between 56°N and 50°N along 145°W between 3 July and 9 July 1998.

Fish were placed in a holding tank with running seawater after capture, and only fish observed to be in good condition were tagged. Fish were placed either in a wooden tagging cradle or on a damp foam pad. The tags were attached to the fish just anterior to the dorsal fin using two 76 mm nickel pins. The pins were inserted through 6 mm diameter plastic disks (as washers or baffles, to prevent the pin head from cutting through the potting material), then through the two holes in the tag, and then through the dorsal musculature of the fish. On the other side of the fish, the pins were inserted through 20 mm or 16 mm diameter red-and-white Petersen disk tags. The ends of the pins were then twisted into knots lying flush against the disks. The tagging procedure generally took one to two minutes. After tagging, fish were immediately dropped over the side of the vessel on two cruises. Aboard the other vessel, fish were observed for 2–15 min in a recovery tank before being dropped over the side. After release on two vessels, fish were visually observed to swim away quickly. One tagged sockeye salmon swam counterclockwise in a 4–5 m diameter circle before moving away. On the third vessel, fish were released at night, and no observations were possible.

To maximize probability of recapture, only fish judged to be maturing and likely to be intercepted by coastal or freshwater fisheries were tagged. Maturity was based primarily on size; previous sampling on research cruises indicated that sockeye, chum, and chinook salmon and steelhead trout with fork lengths greater than 500 mm are likely to be maturing. All pink and coho salmon are maturing after one year at sea. Likelihood of recapture of a tagged individual was based on known ranges of stocks determined by previous tagging experiments (Myers *et al.*, 1996) and on expected activity of coastal fisheries for those stocks. In the Bering Sea, only chum salmon considered to be of Japanese origin were tagged. Japanese origin was judged by scale criteria (determined by the Fisheries Agency of Japan), where counts of circuli in the first and second ocean years were used to distinguish Japanese from Russian, Alaskan, and Canadian chum salmon.

A total of 55 salmonids was tagged, including six sockeye and one coho salmon in the Gulf of Alaska and eastern North Pacific in May. In June, 12 steelhead trout in the central North Pacific and in July, 23 chum salmon in the Bering Sea were tagged. At 48°30′N, 165°W one sockeye salmon was tagged and 12 salmonids (3 sockeye, 1 chum, 4 pink, 3 coho, and 1 steelhead) were tagged in July along a 145°W transect in the Gulf of Alaska.

Interpretation of data

Temperature data recorded by recovered data storage tags were compared to CTD, XBT, and other oceanographic data collected during the cruises of the tagging vessels in 1998 and previous years. Data from fish tagged in the Gulf of Alaska were also examined in relation to data collected from two drifting buoys and one stationary buoy in the northern Gulf of Alaska and to a collection of SST data (Global Telecommunications System (GTS) surface observations from the US Navy's Fleet Numerical Meteorology and Oceanography Center, available from the Pacific Fisheries Environmental Laboratory, NMFS).

Distances travelled between release and recovery sites were calculated as great circle distances between the two points. For the coho salmon and one chum salmon (tag 271), great circle routes would pass over landmasses. In these cases, great circle distances were calculated for two segments of hypothetical migration routes via Unimak Pass (the coho) and Soya Strait (the chum), to indicate more accurately minimum distances travelled.

Because the pink salmon and steelhead were at large for only 3–5 weeks when changes in daylength were small, periods of darkness were estimated by approximate times of sunrise and sunset at a single intermediate point between the sites of release and recovery over on the times of tag deployment. Sunrise and sunset times at release and recovery locations differed by only 8–15 min. The chum and coho salmon were at large for longer periods when daylength changed more rapidly, and daylength also changed over larger latitudinal ranges between release and recovery. For these tags, we used sunrise and sunset times for additional intermediate points interpolated at three-week intervals along straight lines between release and recovery sites.

F-tests for differences in variance and *t*-tests (assuming unequal variances) for differences in means were performed to assess significance of differences between daytime and night-time temperatures.

RESULTS

To date, eight tags have been recovered (Fig. 2; Table 1). Three salmonids, tagged in the Gulf of Alaska, were recovered in Alaska: a pink salmon at

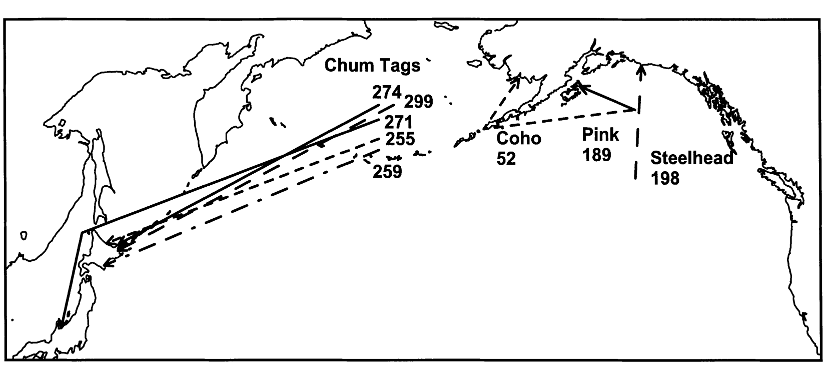


Figure 2. Map of release and recovery locations for eight salmonids tagged with temperature-recording tags in the Bering Sea and Gulf of Alaska in 1998. Lines connect release and recovery sites and do not indicate actual routes travelled. Actual routes are not known. Numbers refer to tag number.

Table 1. Release and recovery information for eight salmonids tagged with temperature-recording tags in the North Pacific Ocean and Bering Sea in 1998 and recovered in Alaska and Japan. SST = sea surface temperature at release. Age determined from scale sample taken at release. Days = number of days fish was at large after tagging. Distance = great circle distance between release and recovery points (for Tag 52, two segments via Unimak Pass; for Tag 271, two segments via Soya Strait). Speed = directional speed, great circle distance divided by days at large. Data points = temperature data points recorded while the fish was at large and do not include data before release or after recovery.

		Release					Recovery									
Tag No.	Species	Date	Location	SST (°C)	Length (mm)	Age	Date	Location	Days	Distance (km)	Speed (km day^{-1})	Data Points	Data Interval	Length (mm)	Weight (kg)	Sex
189	Pink	7/3/98	G. of Alaska 55°59′N 145°00′W	11.0	495	0.1	7/24/98	Afognak Island 58°06′N 152°20′W	21	501	35.7	4063	7.5′		1.4	
198	Steelhead	7/9/98	G. of Alaska 49°58′N 144°58′W	10.9	690	2.3	8/14/98	Copper R. Delta 60°13′N 144°40′W	36	931	25.9	6909	7.5′		3.4	M
52	Coho	7/3/98	G. of Alaska 55°59′N 145°00′W	11.0	592	1.1	8/24/98	Togiak Bay 59°02′N 160°20′W	52	1858	23.8	5857	15′			M
259	Chum	7/3/98	Bering Sea 52°30′N 179°30′W	7.4	622	0.3	9/4/98	Tokachi R. mouth 42°39′N 143°37′E	62	2942	46.7	6011	15′	650	3.0	M
274	Chum	7/7/98	Bering Sea 56°30′N 179°30′W	6.9	680	0.4	9/24/98	Shiretoko Peninsula 44°19′N 145°21′E	79	2779	35.2	3782	30′	716		M
299	Chum	7/12/98	Bering Sea 56°30′N 177°30′W	7.1	577	0.3	10/5/98	Shibetsu, Nemuro Strait 43°41′N 145°09′E	85	2969	34.9	4059	30′	590	2.4	F
255	Chum	7/4/98	Bering Sea 53°30′N 179°30′W	5.9	560	0.3	10/10/98	Yubetsu, Okhotsk 44°13′N 143°40′E	98	2845	28.9	4680	30′	610	2.1	M
271	Chum	7/6/98	Bering Sea 55°30′N 179°30′W	6.3	592	0.3	10/31/98	Sho R., Honshu, Sea of Japan 36°47′N 137°05′E	117	3997	34.1	5607	30′	610	1.8	M

Afognak Island after 21 days; a steelhead trout at the Copper River Delta after 36 days; and a coho salmon in Togiak Bay after 52 days. Five chum salmon, tagged in the Bering Sea, were recovered in Hokkaido (on the Pacific coast after 62 days, on the Nemuro Strait coast after 79 and 85 days, and on the Okhotsk Sea coast after 98 days) and Honshu (in a river on the Sea of Japan after 117 days). Ambient temperatures were recorded every 7.5 min for the pink salmon and steelhead, every 15 min for the coho and one chum salmon, and every 30 min for four chum salmon. The number of data points collected ranged from 3782 to 6909. Temperatures at known points (points of release, recovery, and postrecovery induced marks) matched those recorded independently (e.g. SST at fishing stations, SST near recovery areas where available). When calibrated in ice water baths and at room temperature, recovered tags correctly recorded temperatures.

Figures 3–5 show that all fish did not change ambient temperature for between four and 21 days immediately after release. Thermal profiles for the release areas (Fig. 6) show that temperatures corresponding to the ambient range indicated by the tags occur at 0–20 m. This indicates that the fish were remaining in or near surface waters (top 20 m) for an extended period, with few descents.

After the period of apparently limited temperature change, all fish showed frequent short-term movements between warmer and cooler temperatures, and this behaviour constituted the bulk of all data collected. We refer to the short-term (minutes to hours) movement between warmer and cooler water as 'descents'. While we lack pressure data and cannot demonstrate conclusively that the short-term drops in temperature represent descents, we believe this is more parsimonious than assuming that fish are encountering surface patches of substantially different temperatures

Figure 3. Ambient temperatures recorded from three salmonids tagged in the Gulf of Alaska and recovered in Alaska. Shaded bars indicate approximate hours of darkness.

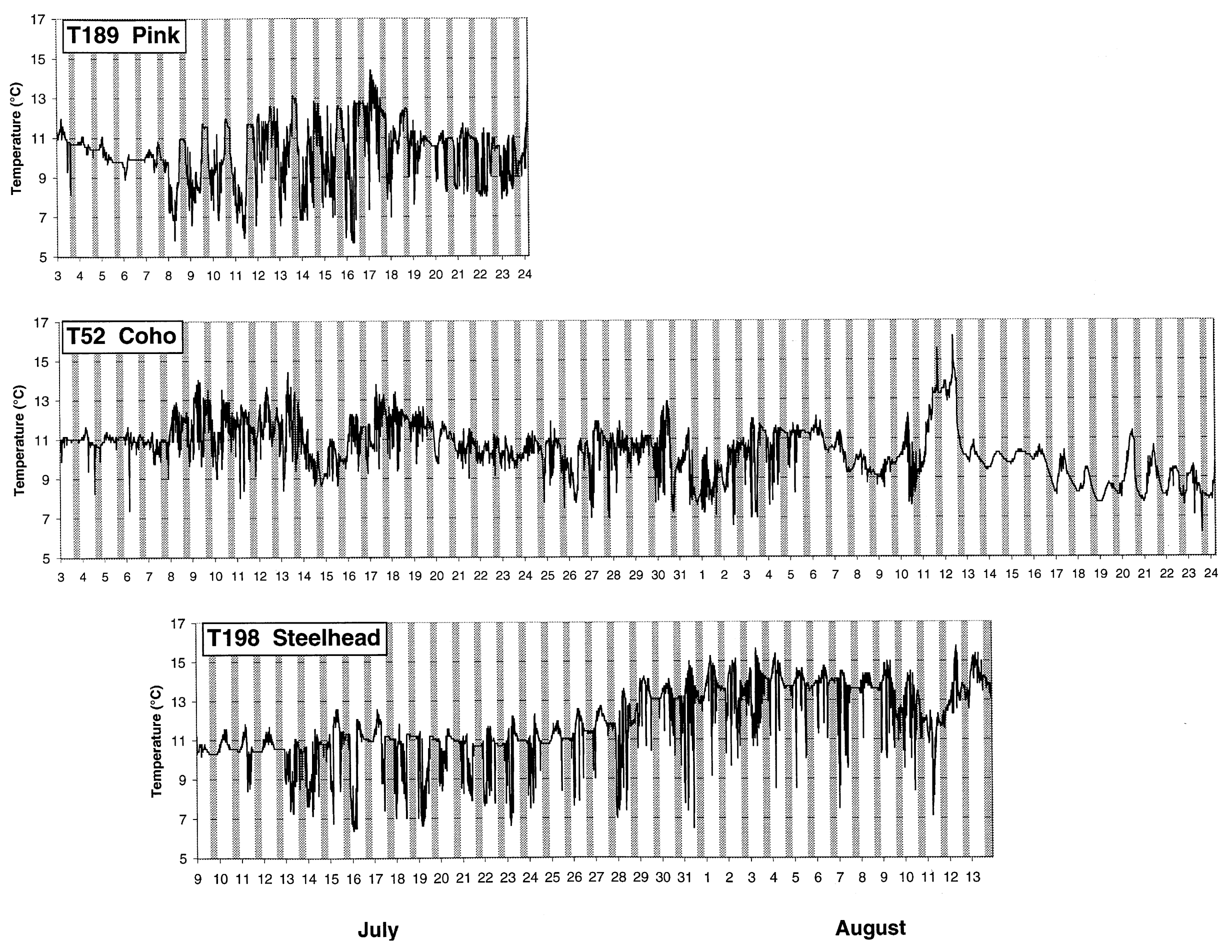
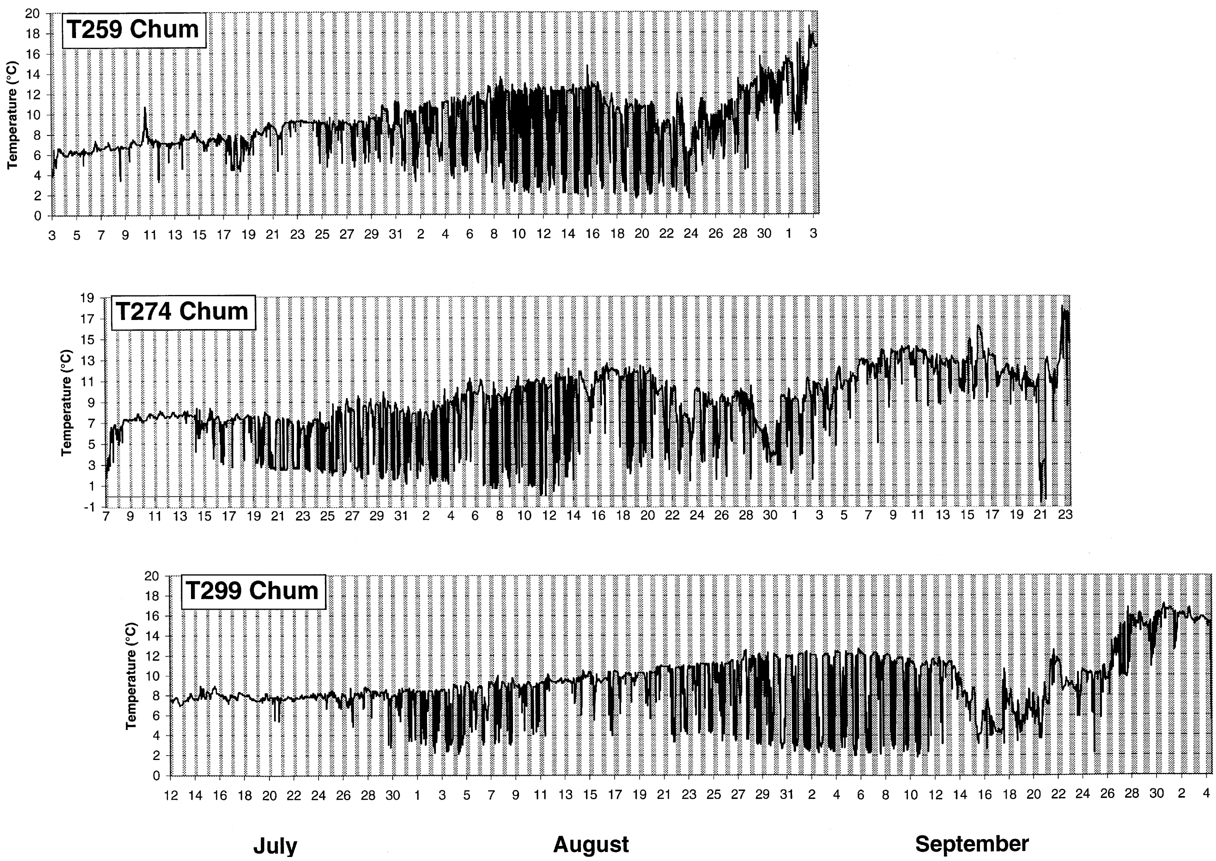


Figure 4. Ambient temperatures recorded from three chum salmon tagged in the Bering Sea and recovered on the Pacific and Nemuro Strait coasts of Hokkaido. Shaded bars indicate approximate hours of darkness.



with such frequency. Temperatures in the range of the cooler temperatures encountered in daytime early in the migrations occurred at ≈20–60 m at the release locations (Fig. 6). For all fish (except the one coho salmon), the data show fairly constant, higher temperatures at night, and more variable temperatures during the day, with movements between warmer and cooler waters ($P < 0.001$; Table 2). This may represent a normal pattern of moving to surface waters (top 20 m) at night, possibly for feeding, and descending to deeper, cooler waters during the day, but with frequent ascents to warmer waters. In the initial few days of 'normal' behaviour, when the fish are most likely to experience sea temperature profiles similar to those recorded at release locations, temperature data can be converted to estimated fish depths over time. Data of this type for the pink salmon and steelhead show the daily frequency and extent of vertical excursions (Fig. 7).

Standard deviations of temperatures were significantly greater during daytime than at night, which reflects more frequent daytime descents ($P < 0.001$ for all species except coho; Table 2). Daytime average temperatures were significantly lower than night-time averages for all species except coho, also reflecting more frequent descents during the day. Daytime maxima were similar to night-time maxima for chum and the coho salmon and the steelhead, while they were cooler for the pink salmon (Figs 3, 4, 5). This indicates that after descending, all fish but the pink salmon were returning at some point during the day to the same level they occupied at night, probably near the surface (top 20 m).

Percentages of time each fish spent at different temperatures may not be strictly accurate, especially for the longer data intervals, but the data indicate that most fish spent the great majority of their time within a range of only four or five °C (Table 3). The fish tagged in the Gulf of Alaska (coho, pink, and steelhead) experienced warmer average temperatures (9–12°C) than the chum salmon tagged in the Bering Sea (7–9°C; Tables 2 and 3). The chum salmon were also

Figure 5. Ambient temperatures recorded from two chum salmon tagged in the Bering Sea and recovered on the Okhotsk coast of Hokkaido and Japan Sea coast of Honshu. Shaded bars indicate approximate hours of darkness.

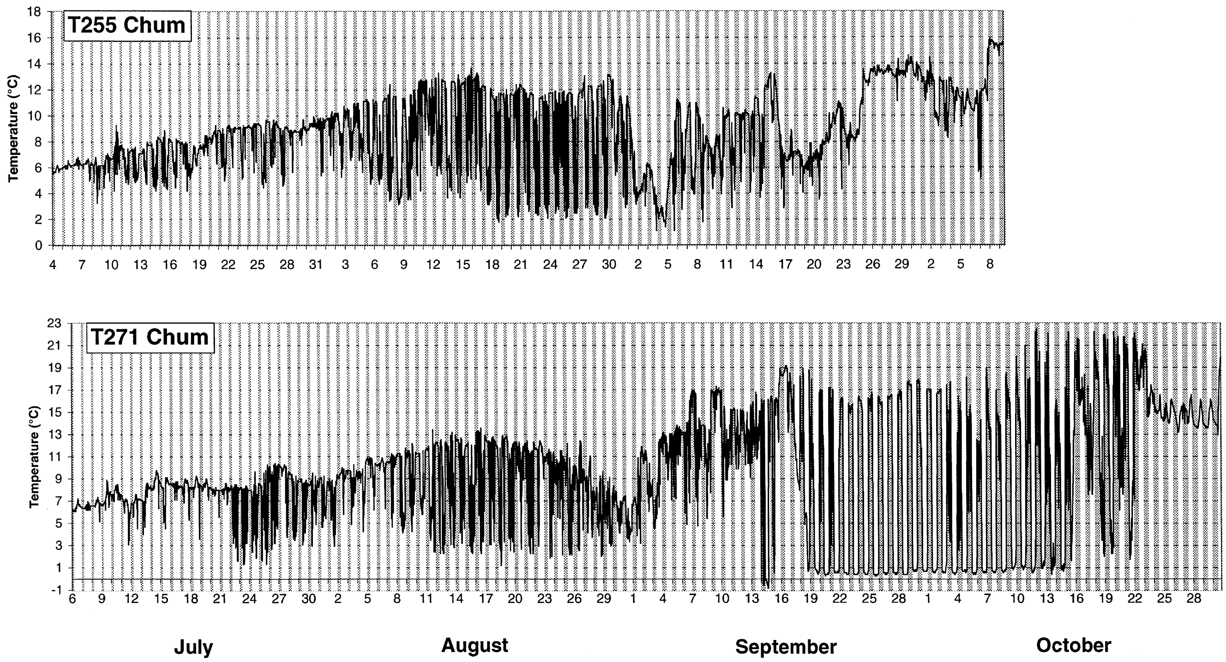
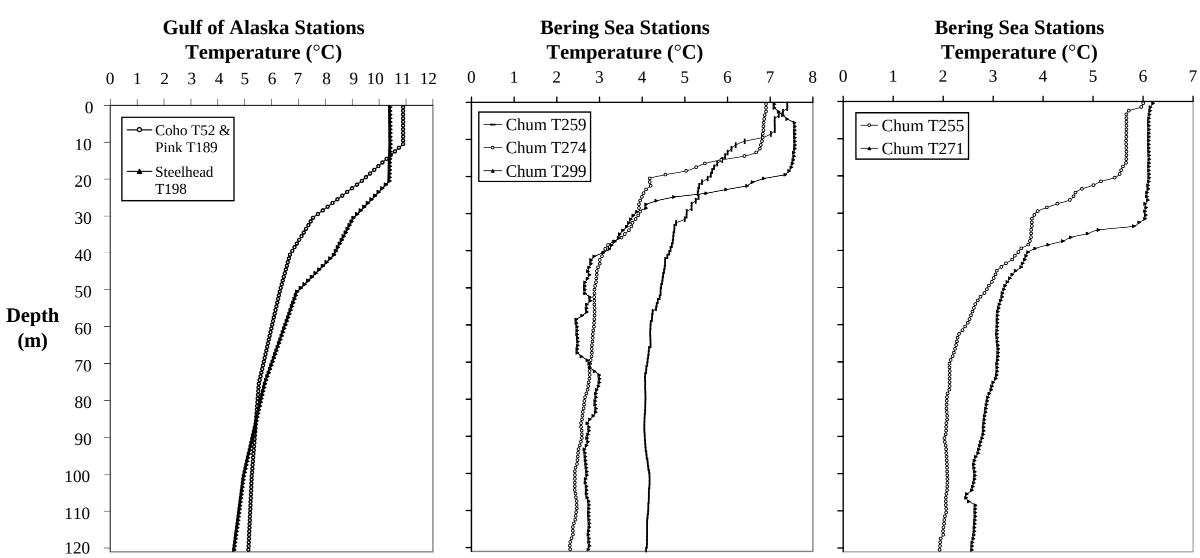


Figure 6. Temperature profiles at fishing stations where fish with temperature-recording tags were released.



found at a wider range of temperatures (−1°C–22°C vs 5–15°C). This reflects the different oceanographic regions encountered by the fish, and may also indicate species differences. Several of the tags on chum salmon recorded very cold temperatures (−1°C to 1°C), as well as quite warm temperatures (17–22°C) in the final phases of migration.

DISCUSSION

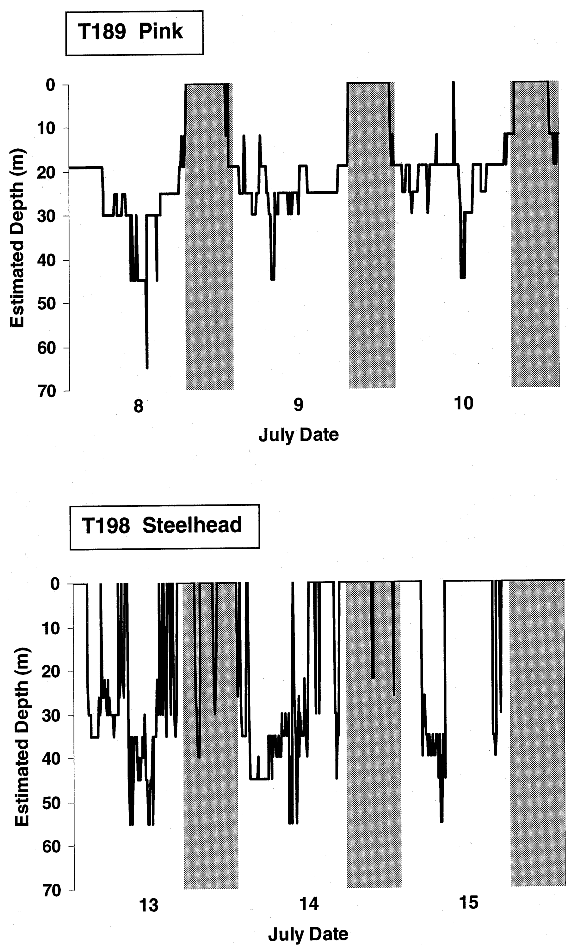
Our recordings of temperature with Pacific salmon species indicate that tagging modifies the behaviours of fish for a period after tag application and that diurnal vertical migration patterns are more developed than had been recognized. Data from all eight fish

Table 2. Means, standard deviations, maximum and minimum temperatures for eight temperature data tags. Statistics exclude data from initial 4–21 days of adjustment to tagging trauma. n = number of data points. *** = significant difference between day and night values ($P < 0.001$) from t-tests (assuming unequal variances) for differences in means, and from F-tests for differences in variance.

	Tag 189 – Pink salmon *16 days, 7.5 min intervals*			Tag 198 – Steelhead *32 days, 7.5 min intervals*			Tag 52 – Coho salmon *47 days, 15 min intervals*			Tag 259 – Chum salmon *41 days, 15 min intervals*		
Temp. (°C)	Day n = 2189	Night n = 896	All n = 3085	Day n = 4088	Night n = 2048	All n = 6136	Day n = 2992	Night n = 1547	All n = 4539	Day n = 2296	Night n = 1622	All n = 3,918
Mean	9.75	11.45***	10.24	11.88	12.18***	11.98	10.45	10.16***	10.35	8.60	10.76***	9.49
SD	1.59	0.91***	1.62	2.04	1.25***	1.82	1.36	1.38	1.38	3.18	2.07***	2.97
Maximum	14.41	13.13	14.41	15.77	14.36	15.77	16.21	15.57	16.21	18.62	17.84	18.62
Minimum	5.70	8.78	5.70	6.38	8.54	6.38	6.62	6.24	6.24	1.61	4.46	1.61

	Tag 274 – Chum salmon *71 days, 30 min intervals*			Tag 299 – Chum salmon *67 days, 30 min intervals*			Tag 255 – Chum salmon *93 days, 30 min intervals*			Tag 271 – Chum salmon *100 days, 30 min intervals*		
Temp. (°C)	Day n = 2055	Night n = 1356	All n = 3411	Day n = 1781	Night n = 1424	All n = 3205	Day n = 2620	Night n = 1854	All n = 4474	Day n = 2649	Night n = 2176	All n = 4,825
Mean	7.93	9.85***	8.69	8.34	10.55***	9.32	7.99	10.18***	8.90	7.30	12.56***	9.67
SD	3.58	2.82***	3.43	3.49	2.60***	3.31	2.94	2.55***	2.98	5.14	4.24***	5.43
Maximum	18.08	17.68	18.08	17.18	16.79	17.18	15.66	15.92	15.92	21.11	22.51	22.51
Minimum	–0.38	–0.67	–0.67	1.84	2.24	1.84	1.11	2.07	1.11	–0.83	–0.55	–0.83

Figure 7. Estimated depths and daily activity of pink salmon and steelhead trout during the first three days of 'normal' behaviour after recovery from presumed tagging trauma. Depths were estimated using temperature profiles recorded several days earlier at fishing stations where fish were released. Shaded bars indicate approximate hours of darkness.



show a period of relatively constant temperatures, close to those of surface temperatures at the time of release, lasting from 4 to 21 days. This pattern was found in fish recovered from the Gulf of Alaska and from the Bering Sea. Similar periods of constant temperature were not found later in the data, except for some instances when fish were nearing the coast. We believe this is a period of recovery from the trauma of capture, tagging, and release and adjustment to the tag attachment. Possible tagging trauma has been identified in other studies. Holland *et al.* (1990), for example, noted a 4–6 h 'postcapture recovery period' in blue marlin (*Makaira nigricans*) tagged with acoustic tags, where the fish dove into and remained in the upper layers of the thermocline before resuming what was described as more normal behaviour with vertical excursions and horizontal swimming. The tracking, however, was limited to 24–42 h, so longer-term changes could not be assessed. In an ultrasonic telemetry study, adult chinook salmon in British Columbia coastal waters went through a period of reduced activity, probably passively sinking, immediately after release (Candy and Quinn, 1999). Most returned to 'normal' (consistent) behaviour after 6–8 h, though in some cases fish did not start a pattern of consistent behaviour for over 24 h. Surgically and gastrically implanted radio transmitters were found to significantly reduce swimming speeds and increase vulnerability to a freshwater predator in juvenile chinook salmon in hatchery tests (Adams *et al.*, 1998). As there are no data on the behaviour of untagged fish, the possibility exists that immediate postrelease behaviour is 'normal' and that regular patterns of diurnal behaviour are aberrant reactions to the presence of the tag. However, similar interpretations of effects in other species, the normal sequence of healing, the large amount of data showing regular diurnal patterns, and long-held assumptions and evidence about daily cycles of salmon behaviour all indicate that the initial post-tagging behaviour is the abnormal one. Therefore, data collected from short-term tagging studies, such as with acoustic tags, may be subject to tagging effects that may cause misinterpretation of the fish's behaviour (see Boehlert, 1997), particularly in interpreting at least vertical movement and temperature data from ultrasonic tagging studies where fish are followed for only 1–5 days.

Because the data storage tags used in this study were not implanted in the stomach or abdomen, there was no surgical incision or artificial stomach fullness, and because they are light, their effect on drag and fish buoyancy is probably not large. The estimated migration rates (23.8–46.7 km day^{-1}, net) are within the ranges calculated by species, month, and recovery areas from high seas tagging data (Ogura, 1994), which indicates that the long-term effect of these tags on travel speed was not substantially different from that of regular disk and tube tags. The entire capture and tagging procedure may be more responsible for the trauma than the particular type of tag or attachment. The relatively constant temperatures recorded during initial recuperation do not necessarily mean that the fish are passively floating. Fish in ultrasonic-tracking studies show considerable consistent directional horizontal movement after tagging (Quinn *et al.*, 1989; Ogura and Ishida, 1992, 1995; Ogura, 1994). During this period, the fish in our study may be actively swimming and are simply unwilling or unable to

Table 3. Percentage of time at each temperature for eight temperature-recording tags. Statistics exclude data from initial 4–21 days of adjustment to tagging trauma. *n* = number of data points.

	Tag 189 – Pink Salmon *16 days*			Tag 198 – Steelhead *32 days*			Tag 52 – Coho Salmon *47 days*			Tag 259 – Chum Salmon *41 days*		
Temp. (°C)	Day *n* = 2189	Night *n* = 896	All *n* = 3085	Day *n* = 4088	Night *n* = 2048	All *n* = 6136	Day *n* = 2992	Night *n* = 1547	All *n* = 4539	Day *n* = 2296	Night *n* = 1622	All *n* = 3918
1										0.5	0	0.3
2										5.3	0	3.1
3										4.4	0	2.6
4										4.4	0.2	2.7
5	0.8	0	0.6							6.7	0.7	4.2
6	3.8	0	2.7	1.2	0	0.8	0.0	0.1	0.1	8.8	1.7	5.8
7	8.4	0	5.9	3.4	0	2.3	2.8	3.3	3.0	8.2	2.3	5.8
8	20.6	0.1	14.7	7.7	0.1	5.2	10.8	17.1	12.9	15.9	9.7	13.3
9	20.1	6.5	16.1	4.3	0.3	2.9	20.0	24.2	21.4	12.5	21.4	16.2
10	24.5	35.0	27.6	13.0	23.7	16.6	33.1	25.4	30.5	9.9	25.3	16.3
11	14.5	29.7	18.9	23.0	29.4	25.1	20.3	20.3	20.3	8.8	12.4	10.3
12	5.3	24.8	11.0	12.4	7.1	10.6	8.6	6.4	7.9	7.9	17.7	12.0
13	1.8	3.9	2.4	17.8	35.3	23.6	3.6	3.0	3.4	2.5	2.0	2.3
14	0.2	0	0.2	15.0	4.1	11.3	0.6	0.1	0.4	2.3	1.6	2.0
15				2.3	0	1.5	0.1	0.1	0.1	0.8	2.0	1.3
16							0.0	0	0.0	0.5	1.8	1.0
17										0.4	1.1	0.7
18										0.1	0	0.1

	Tag 274 – Chum salmon *71 days*			Tag 299 – Chum salmon *67 days*			Tag 255 – Chum salmon *93 days*			Tag 271 – Chum salmon *100 days*		
Temp. (°C)	Day *n* = 2055	Night *n* = 1356	All *n* = 3411	Day *n* = 1781	Night *n* = 1424	All *n* = 3205	Day *n* = 2620	Night *n* = 1854	All *n* = 4474	Day *n* = 2649	Night *n* = 2176	All *n* = 4825
−1	0.0	0.1	0.1							0.5	0.3	0.4
0	0.6	0.3	0.5							19.4	1.0	11.1
1	4.2	0.4	2.7	0.3	0.0	0.2	0.6	0.0	0.4	3.9	0.8	2.5
2	9.8	1.3	6.4	5.8	0.1	3.3	3.5	1.1	2.5	3.5	1.2	2.5
3	5.9	2.8	4.7	9.8	0.1	5.5	4.8	0.7	3.1	4.5	0.5	2.7
4	3.5	0.7	2.4	6.1	2.1	4.3	5.4	1.0	3.6	5.4	1.0	3.4
5	5.4	0.7	3.5	4.5	1.9	3.3	11.1	2.3	7.5	5.1	1.1	3.3
6	6.9	4.5	5.9	6.9	2.7	5.0	15.1	6.2	11.4	4.9	2.3	3.7

Table 3. *(Continued)*

Temp. (°C)	Tag 274 – Chum salmon *71 days* Day n = 2055	Night n = 1356	All n = 3411	Tag 299 – Chum salmon *67 days* Day n = 1781	Night n = 1424	All n = 3205	Tag 255 – Chum salmon *93 days* Day n = 2620	Night n = 1854	All n = 4474	Tag 271 – Chum salmon *100 days* Day n = 2649	Night n = 2176	All n = 4825
7	11.1	13.2	11.9	7.6	5.2	6.5	11.6	8.5	10.3	4.9	3.9	4.4
8	9.8	10.8	10.2	13.7	14.3	14.0	12.2	10.9	11.7	8.2	7.2	7.7
9	8.7	16.9	11.9	16.8	15.7	16.3	12.9	13.1	13.0	7.0	6.7	6.8
10	10.0	13.3	11.3	9.0	15.7	12.0	5.5	11.8	8.1	7.2	8.8	7.9
11	10.9	13.2	11.8	8.5	18.0	12.7	5.2	18.2	10.6	5.7	8.9	7.2
12	7.9	10.4	8.9	3.1	11.5	6.9	5.3	14.7	9.2	4.9	10.3	7.4
13	4.5	6.6	5.4	0.9	0.4	0.7	5.4	8.0	6.5	3.5	7.8	5.4
14	0.5	2.1	1.1	0.6	2.5	1.4	0.5	0.9	0.6	2.7	6.9	4.6
15	0.2	0.9	0.5	3.5	6.0	4.6	1.0	2.5	1.6	3.0	8.0	5.3
16	0.0	1.0	0.4	2.6	3.7	3.1				3.1	10.1	6.2
17	0.0	0.8	0.4	0.3	0.0	0.2				0.9	4.3	2.4
18	0.0	0.0	0.0							0.8	4.1	2.3
19										0.6	1.7	1.1
20										0.2	1.7	0.8
21										0.0	1.1	0.5
22										0.0	0.4	0.2

descend. It is possible that horizontal-movement data from ultrasonic tracking represent more normal behaviour than the vertical-movement data.

In the first few days after tagging, the behaviour of the fish discussed in this report was like that reported in some ultrasonic tagging studies, that is, remaining near the surface. (Most of the fish in telemetry studies made deep descents immediately after release, but then returned to the surface. Only three fish in this study displayed slight to deeper descents.) After a period of 4–21 days, however, all fish began regular daily patterns of descents during the day and spending nights near the surface, probably less than 20 m. This sequence of behaviour was comparable to that of a chum salmon reported by Ishida *et al.* (1997), which they tagged with a depth-recording data storage tag in the southern Kuril Islands. After tagging, the fish underwent a 3.5-day period of descents and ascents that did not have a clear diel pattern. For the following 18 days when data were recorded, the fish spent nights in surface waters (mostly 0–10 m) with few descents, and days moving vertically between the top 10 m and depths of 40–60 m.

The day–night differences in the stored temperature data conform to previous assumptions that salmon move into surface waters at night, and descend to deeper, cooler waters during the day. However, after descents during the day, most fish returned to near-surface waters, except for the pink salmon, which usually remained in cooler waters throughout the day. The coho salmon sometimes continued descents through the night, and some portions of its daily record show little change in temperature, perhaps representing times of directed travel, with little feeding, or travel through a well-mixed water mass. Steelhead have been assumed to remain in surface waters (0–20 m; Burgner *et al.*, 1992), but our data demonstrate that they make numerous descents during the day to waters 3–5°C cooler than the surface (perhaps 40–60 m deep). This behaviour is similar to that of the pink and coho salmon. Because sample sizes are small, the behaviour of individual fish may not apply to each species in general.

Daylight is quite long (17 h between sunrise and sunset, 19 h between sunrise and sunset twilight) at the season and latitudes where fish were tagged. Diurnal cycles at all stages of migration seemed to be linked with sunrise and sunset times and not with beginning and end of twilights. Daylength became much shorter for the chum salmon as they migrated over several months to lower latitudes, and onset and end of daily surface-orientated and descending phases changed with changing times of sunrise and sunset. Occurrence of full moons did not show a discernible effect on temperature data. Weather is often overcast in the North Pacific, and this may have obscured any lunar cycle effects, if they exist.

The diurnal cycle probably results from several driving forces, including optimal feeding, thermoregulation, searching for orientation clues during migration, and predator avoidance. Many of the organisms on which salmon feed, such as euphausiids, amphipods, and squid, migrate into the upper part of the water column at night; this is particularly true of euphausiids, which are most prevalent in salmon stomachs at night (Pearcy *et al.*, 1984; Davis *et al.*, 1998). The daytime descents indicated by our findings could be continuing to follow and feed on the same organisms as they move deeper. In a 24 h study of feeding by sockeye, pink, and chum salmon, Davis *et al.* (1998) found that all three species likely fed throughout the day. Sockeye and pink stomachs had a fullness peak near sunset, but pink salmon had a second peak at noon and chum salmon stomachs were most full in the afternoon. Variations in prey composition through the day (Pearcy *et al.*, 1984) support the idea that the vertical excursions are trophic in nature.

The relatively constant temperatures displayed during the night by most of the tagged fish in our study do not necessarily mean that the fish are remaining in one place. They may be actively swimming and selecting waters in a narrow temperature range, presumably near the surface. Ogura and Ishida (1995) found that swimming speed and direction of ultrasonically tagged salmon at night were about the same as during the day on the high seas. However, sockeye in coastal waters were slower at night, though not stationary (Madison *et al.*, 1972; Quinn, 1988), and steelhead in coastal waters did not seem to be actively swimming, but drifting with tidal currents (Ruggerone *et al.*, 1990).

The latter stages of migration show a cessation of large temperature changes for the coho salmon (about 19 days), steelhead (2–3 days), and some chum salmon. This may be a period of directed movement and possible end to feeding descents, or may occur in areas with well-mixed surface waters of homogeneous temperatures. For some fish, this may be in coastal waters. Steelhead tracked in coastal waters by ultrasonic telemetry remained in surface waters (above 6 m, Ruggerone *et al.*, 1990). In the case of the coho, it may coincide with transit of the south-eastern Bering Sea.

Oceanographic data recorded on data storage tags can be used to infer general routes of migration by comparing them with contemporaneous data from other sources and with known oceanographic features. Examination of temperatures charted by days shows obvious changes in maximum (i.e. surface) temperatures and in daily temperature ranges as the fish move through different water masses (Figs 3, 4, 5). For example, the pink salmon and steelhead show similar patterns of movement through oceanographic regions of the Gulf of Alaska. Initially in the central gyre (maximum temperatures of 11–12°C), they cross the slightly warmer surface waters of the Alaska Current (12–13°C maxima), then move into cooler coastal waters. The picture is more complex for the chum and coho salmon. In future analyses we plan to estimate their routes through likely water masses.

Several of the chum salmon encountered very cold waters (−1°C to 1°C), possibly several hundred metres deep. Similar temperatures (0–2°C) have been recorded at depths of 50–275 m by tags, recording temperature and depth, placed on Japanese chum salmon, and several studies have observed trawl catches of chum salmon at depths of several hundred metres (Ueno, 1992; Radchenko and Glebov, 1998). However, it is also quite possible that the fish were encountering cold upwelling in the Kurils (2°C near surface in midsummer, Shuntov *et al.*, 1993) or cold water at relatively shallow depths near the southern end of Kamchatka (2°C at ≈70 m in late summer; Antonov *et al.*, 1998). But the daily alternation of warm and cold temperatures displayed by the chum salmon carrying tag 271 is likely migration from the surface to deep waters. Ueno (1992) noted that trawl (i.e. near-bottom, 150–460 m) catches of chum were much higher during the day, the time of day when chum salmon 271 was experiencing cold temperatures. Radchenko and Glebov (1998) speculated that the tendency of migrating chum to move to deeper, cooler water might be to conserve energy while gonads were in the final stage of maturation.

We suspect the distribution of data points (time spent) at different temperatures (Table 3) reflects primarily surface temperatures and temperatures at depths to which salmon may commonly descend (possibly 30–60 m) in areas that salmon use for feeding and migration. Given the frequency of descents and ascents during the day and the differences in daily temperature ranges found during the migrations, it seems less likely that salmon are selecting particular temperatures. An exception is the chum salmon carrying tag 271, which may have selected low temperatures each day to avoid prolonged exposure to high temperatures in surface waters. The use of these data in bioenergetics and modelling studies will improve our ability to estimate more accurately the growth and production of species of Pacific salmon and steelhead.

Welch *et al.* (1995, 1998a,b) have postulated thermal limits and SST as determinants of salmon distribution. They found sharp upper limits of SST defining the southern boundaries of salmon and steelhead distribution in spring. More detailed analyses of sockeye salmon and steelhead trout indicated thermal limits changed by month, region of the North Pacific, and decade (Welch *et al.*, 1998a,b). They cite the need for data to understand biological reasons for any thermal limits that may restrict salmon distribution and make them susceptible to possible warming of the North Pacific owing to global climate change. Our data provide significant direct information about thermal habitat available to migrating salmon and steelhead. The results indicate that in the course of their migrations, salmon and steelhead experience a wide range of temperatures, probably through vertical movements (within the top 30–60 m).

Our study has shown that several species of salmonids are capable of carrying data storage tags, that recoveries of the tags can be achieved (even when a limited number of tags are used and even when fish are released far from shore), and that return rates justify further effort. While selection of fish likely to be mature (to minimize time at liberty) and targeting of species and stocks likely to be caught probably contributed to the recovery rate, the large size (relative to disk and dart tags) and high-tech look of the tags also may have stimulated recovery and returns. A similar phenomenon was noted by Karlsson *et al.* (1996). The scientific data retrieved from the tags provide a wealth of information on how these animals behave in the ocean. Further research should take advantage of improved tag technology and increase the number of environmental features measured by the tags, incorporating sensors to measure depth, salinity, light, and other parameters.

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