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[Article]

Upper Thermal Limits to Migration in Adult Chinook Salmon: Evidence from the Klamath River Basin

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Abstract.—Temperature-sensitive transmitters and archival tags allowed precise measurement of adult Chinook salmon *Oncorhynchus tshawytscha* responses to high water temperatures and other environmental variables in the Klamath River basin during 2004 and 2005. Mean daily river temperatures upon initiation of upriver migration by adult Chinook salmon after a period of thermally induced migration inhibition ranged from 21.8°C to 24.0°C (mean = 22.9°C). During the first week (168 h) of migration, mean average body temperature was 21.9°C, mean average minimum daily body temperature was 20.6°C, and mean average maximum daily body temperature was 23.1°C. Temperatures above these levels appeared to completely block migration in almost all circumstances. Migration was inhibited at lower mean daily river temperatures during periods of increasing river temperatures than during periods of declining river temperatures. The ability of adult Chinook salmon to correctly gauge the onset of periods of declining or inclining river temperature is a vital mechanism for taking advantage of brief thermal windows for upriver migration. Weather fronts were responsible for periods of declining river temperature, but no precipitation or consistent drops in atmospheric pressure were associated with these weather fronts or with fish movements. The associated decrease in light levels, however, appeared to serve as an indicator of impending reductions in river temperatures for adult Chinook salmon. Changing river discharge had a negligible influence on migration behavior, and hypoxia sufficient to inhibit upriver migration (i.e., dissolved oxygen < 5 mg/L) never occurred during the study. The upper thermal limits to adult Chinook salmon migration as indicated by results from the Klamath River basin are substantially higher than previously reported in the literature and approached or exceeded the highest ultimate upper incipient lethal values determined for any life stage of this species.

Temperature governs the rate of metabolic processes and profoundly affects the behavior of poikilothermic organisms, including salmonid fishes. Since metabolic rate increases as temperature rises (Fry 1947), greater energy inputs are required at higher temperatures to achieve a given growth rate in juveniles or a given activity level in migrating adults (Brett 1995). Adult salmon migrating in rivers must contend with ambient temperatures during a period when they cease feeding but also require increased energy expenditures due to migration and the final development of gonads. With these added bioenergetic constraints, temperature is especially important in shaping the behavior of salmonid adults during their spawning migrations and ultimately affects their level of reproductive success through multiple pathways (Elliot 1981; Gilhousen 1990; Naughton et al. 2005; Cooke et al. 2006).

Assessing the effect of temperature on the migration behavior of adult salmon requires a consideration of the broader context in which their migration occurs. To successfully complete their spawning migration, adult salmon must balance the costs and benefits associated with a suite of interacting environmental and physiological variables and potential migration behaviors. Our understanding of how these competing variables shape salmon migration can be aided by following their requirements backwards from the ultimate goal—survival of offspring. Survival of offspring is strongly influenced by emergence timing, which is a function of the timing of spawning and the thermal regime during incubation (Brannon 1987). To achieve a spawn timing that results in favorable emergence timing for offspring, adult salmon must arrive on the spawning grounds in suitable condition and with enough time to search and locate favorable spawning sites and mates. To accomplish that task, salmon must complete upriver migration without excessive energetic expenditures, physiological stress, or time delays.

During periods of excessively high water temperatures, migratory movement becomes too energetically and physiologically costly (Brett 1979; Cooke et al. 2006) and salmon must suspend migration and, if possible, must seek and use coldwater thermal refuges (Major and Mighell 1967; Berman and Quinn 1991; Quinn et al. 1997; Hyatt et al. 2003; Goniea at al.

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2006). Knowing the temperature or temperature range at which migration is inhibited is a core component of understanding the effect of temperature on migration behavior. From a management perspective, such knowledge is vital for gauging the effect of river temperatures and management actions that influence temperature, evaluating population persistence, and predicting potential effects of climate change. Ideally, this knowledge would be coupled with data on the optimal temperatures for migration and the consequences of migration at suboptimal temperatures, including causal linkages to prespawn mortality and reduced gonadal fitness.

The upper temperatures at which adult salmon migrate (beyond which migration ceases or is inhibited) represent realized performance within the context of interacting stressors. The temperatures associated with the cessation or inhibition of adult salmon migration have previously been examined by using data from biotelemetry or counting facilities. In general, these studies suggest that the upper thermal limit to migration occurs at temperatures of 19–23°C for all species and races of salmonids and at 21°C for adult Chinook salmon *Oncorhynchus tshawytscha* (Hallock et al. 1970; Stuehrenberg et al. 1978; Stabler et al. 1982; Alabaster 1988, 1989; Bumgarner et al. 1997; Fresh et al. 1999; McCullough 1999; McCullough et al. 2001; Goniea et al. 2006). Partly due to logistical or technological constraints, the resolution of the data leading to these conclusions has been relatively low, and questions also remain about the degree to which the observed cessation of migratory movement was governed by timing of the migration season versus physiological limits. Thus, the upper thermal limits for migration among adult salmonids remained ambiguous.

To improve the general understanding of this topic, I selected the Klamath River basin of northern California (Figure 1) to more precisely examine the upper thermal limit for adult Chinook salmon migration. To measure upper thermal limits to migration, multiyear biotelemetry data sets were used to evaluate migration behavior (initiation, migration rates, and behavioral thermoregulation) starting at river entry in relation to ambient river and fish body temperatures at multiple time scales. Meeting this primary objective required examining the possibility that migratory movement was inhibited by low river discharge or dissolved oxygen. A secondary objective was to evaluate whether changes in other environmental variables besides temperature, such as light intensity, atmospheric pressure, and precipitation, coincided with the initiation of upriver migratory movement.

Study Site

The Klamath River basin is an ideal location for achieving the study objectives. The river basin's climate, geology, and geography result in a high thermal regime, with annual maxima that exceed 26°C (Bartholow 2005; author's personal observation) and thus are above any plausible upper thermal limits to migration. The river system also contains natural- and hatchery-origin runs of Chinook salmon that enter the river and initiate upriver migration every month during April through December, including the hottest summer months of July and August. The main-stem Klamath River and its primary tributary, the Trinity River, are large (mean annual minimum monthly flow = 89 m^3/s in the Klamath River and 19 m^3/s in the Trinity River) and migration blockages due to low flow are relatively unlikely (Jonsson 1991). Additional desirable attributes of the Klamath River include an estuary containing a cold salt wedge (e.g., 14–17°C) with access to the ocean and feasible sites for capturing and tagging fish at the beginning of their riverine migration. The river also contains multiple thermal refuges at the confluences of cool tributaries within its lower reaches (e.g., Blue Creek).

The Klamath River drains approximately 31,000 km^2 in southern Oregon and northwestern California and flows 386 km from the outlet of Upper Klamath Lake (a hypereutrophic, regulated natural lake) to the river's confluence with the Pacific Ocean (Figure 1). Under the Köppen classification (Köppen 1931), climate in the basin is considered Mediterranean, with hot dry summers, high winter rainfall, and coastal summer fog trending inland towards progressively drier and more continental climates. Upriver movement of anadromous fish populations is currently restricted by Iron Gate Dam at river kilometer (rkm) 310 (as measured from the mouth of the Klamath River; Figure 1), which has a large mitigation hatchery. Flow releases at Iron Gate Dam are controlled by the U.S. Bureau of Reclamation (USBR), and the water is withdrawn from the metalimnion, which is cooler in the spring and warmer in the fall than ambient water temperatures (Bartholow 2005). The lower Klamath River is defined as the main-stem reach below the confluence with the Trinity River at Weitchpec, California (rkm 70). The Trinity River also has dams without fish passage, and a large mitigation hatchery is located at rkm 252. Flow releases from the Trinity River dams are controlled by the USBR, with water withdrawn from the cold hypolimnion. Based on catch-per-unit-effort data describing hatchery fish in tribal fisheries, stream-type Chinook salmon enter the river with a bimodal peak in numbers during early June and late July. The more

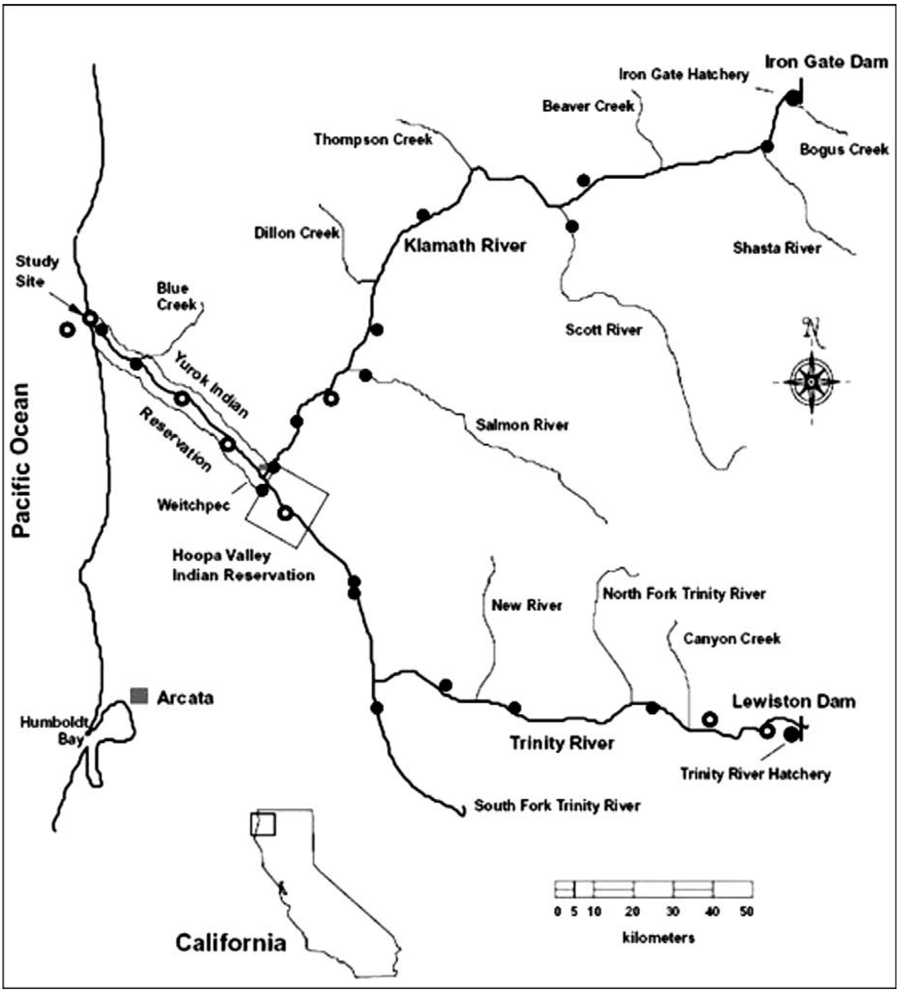

FIGURE 1.—The Klamath River basin of northern California and southern Oregon. Approximate locations of fixed-site listening stations in 2004 and 2005 are designated by solid circles; open circles designate stations used in 2005 only. Iron Gate Dam on the main-stem Klamath River and Lewiston Dam on the main-stem Trinity River both currently limit the upriver distribution of anadromous fishes within the basin and have large mitigation hatcheries. Inset shows the relative location of the study area in northern California.

abundant ocean-type Chinook salmon runs peak during the first week of September for Klamath River stocks and during mid-September for Trinity River stocks (Yurok Tribal Fisheries Program, unpublished data).

Methods

Tagging and telemetry.—The present investigation was part of a larger biotelemetry study in which adult Chinook salmon were tagged in the lower Klamath River and its estuary during 2002 through 2006. Temperature-sensitive transmitters were used to track the movements and internal body temperatures of adult Chinook salmon throughout their spawning migration in the Klamath River basin. However, due to exclusion criteria (defined in the data analysis section), only data from 2004 and 2005 were used in the present analysis. We used pulsed radio transmitters (Advanced Telemetry Systems [ATS] F1845; 19 mm wide × 51 mm long; 24 g in air) in 2004 and coded sonic transmitters (VEMCO V16T-3 L-S256; 16 mm wide × 73 mm long; 28 g in air) in 2005, which were implanted orally into the stomach of the fish. An archival temperature device (Alpha-Mach iBCod with thermister type Z in 2004 and type 22L in 2005; 22 mm wide × 12 mm long; 9.5 g in air) was attached to the base of each transmitter to record internal body temperature every

60–120 min. Each fish was externally marked with a metal jaw tag. Before deployment, we tested all telemetry transmitters for proper function and tested all archival tags to the manufacturer's specified minimum accuracy (Alpha-Mach iBZ: precision was ±1.0°C, resolution was ±0.125°C; iB22-L: precision was ±0.5°C, resolution was ±0.0625°C) using cold- and warm-temperature water baths with an American Society for Testing and Materials (ASTM) certified thermometer. The rate of tag temperature equilibration is a function of the thermal resistance of the tagged fish, which is presumably a function of surface to volume ratios. For adult Chinook salmon, the time to equilibrate from a water bath of 9–19°C was estimated in a controlled laboratory setting as approximately 0.5 h for a 3-kg fish and 1.0 h for an 11-kg fish (Berman 1990).

Adult Chinook salmon were captured, tagged, and released at the mouth of the Klamath River where the estuary drains into the Pacific Ocean. Fish were captured using drift gill nets. After being quickly cut out of the net, each fish was transported to a nearby live tank (946 L) with circulating river water. Fish were immobilized in a cradle, measured to the nearest 0.5 cm (fork length), tagged with a custom plastic pipe, and released immediately or revived first if necessary. To facilitate quick recovery, no anesthesia was used. Tissue samples were taken from rayed fins and stored in ethanol to allow for genetic analysis to verify racial or stock origin at a later date. All captured Chinook salmon were tagged regardless of the presence or absence of an adipose fin. Fish with severe injury, hemorrhage from the gills, or persistent disequilibrium were not tagged.

A network of fixed-site receivers of various brands (VEMCO VR2, Grant Systems Engineering Orion, Lotek SRX400, and ATS R4000/DCC) were placed throughout the Klamath River basin at strategic locations to continuously monitor fish presence or absence and record internal body temperatures (Figure 1). The spatial relationship of the listening stations allowed migration paths and travel rates to be determined. During 2004, tagged fish were also tracked with mobile manual radio receivers (Lotek SRX400 and ATS R4000) and triangulation procedures, which aided in the recovery of tags after death. Transportation during manual tracking was by truck, jet boat, raft, or airplane, depending on the reach.

Hatchery personnel and those participating in snorkel and boat surveys for live fish and carcasses within the study area were notified of the study to assist in locating tagged Chinook salmon and retrieving archival tags. Flyers were posted throughout the study area to alert anglers of the study, and a US$50 reward was offered for archival tags. Harvest monitoring personnel also assisted with recovering tags from tribal and sport fisheries.

Environmental monitoring.—Ambient water temperatures in the main-stem Klamath River were obtained from temperature recorders operated by the U.S. Geological Survey (USGS) at rkm 13, which were rated in accuracy to within 0.2°C. Water temperature data were available at numerous locations throughout the main-stem Klamath River, but only data from rkm 13 were used because study fish resided downstream from rkm 13 during periods of migration inhibition.

Mean daily river flows (m^3/s) for the Klamath River at rkm 13 were calculated from data (15-min interval measurements) obtained from USGS gauging station 11530500 (USGS 2009). Dissolved oxygen data (mg/L; 30-min interval measurements) were obtained from the Yurok Tribal Environmental Program's multiparameter water quality monitoring station at rkm 13. Mean daily solar radiation (W/m^2) was calculated from hourly land surface data obtained from the California Data Exchange Center for the Maple Creek monitoring site (three-letter identification code = MPC; cdec.water.ca.gov/cgi-progs/staMeta?station_id = MPC) (CDEC 2009). This site is approximately 80 km south of the Klamath River mouth on the same longitude as rkm 20. Even though the MPC site is located in another watershed, its data were considered more accurate for the timing of westward-approaching, synoptic-scale weather events at the Klamath River mouth than data from all other solar radiation sites because of the MPC site's coastal location. Mean daily atmospheric pressure (barometric pressure, mm) was calculated from hourly data obtained from the California Data Exchange Center for the Trinity Camp (~rkm 250 on the Trinity River) monitoring site (TNC; cdec.water.ca.gov/cgi-progs/staMeta?station_id = TNC). No atmospheric pressure data were available from any coastal sites in the area. Daily accumulated precipitation data (cm) were obtained from the California Data Exchange Center for the Klamath River at Orleans (rkm 95) monitoring site (OLS; cdec.water.ca.gov/cgi-progs/staMeta?station_id = OLS). An examination of other monitoring sites throughout the Klamath River basin showed the same July and August precipitation patterns as observed at OLS.

Data analysis.—To limit analyses to Chinook salmon with data relevant to the upper thermal limit to migration, tagged fish were excluded from analysis if they met either of the following criteria: (1) there were no detections beyond the upper terminus of the estuary at rkm 7 or (2) fish initiated upriver migration before the seasonal onset of daily maximum water temperatures at or above 20°C (i.e., spring run) or after the seasonal onset of daily maximum water temperatures less than 20°C (i.e., almost all of the fall run). All other tagged Chinook salmon were included in analysis.

Initiation of upriver migration by tagged Chinook salmon was defined by the date and time of first detection at the Wakel listening station at rkm 7. This site was at the upper terminus of the estuary, and thus it was above the influence of the cold salt wedge. Graphical analysis was used to compare the initiation of upriver migration with mean daily river temperature, instantaneous river temperature (measured at 15-min intervals), mean daily river flow, mean daily solar radiation, mean daily atmospheric pressure, and precipitation. A commonly scaled *y*-axis allowed accurate visual comparison between years. Plotted fish movements were limited to all detections from the time of tagging at rkm 0 to arrival at the Trinity River confluence (approximately rkm 70) or the nearest available detection to reduce visual clutter and because migration inhibition occurred below rkm 70. Migration rates (km/d) in the lower Klamath River were calculated from this portion of the biotelemetry records.

Instantaneous river temperature upon initiation of upriver migration by tagged Chinook salmon was defined as the temperature recording at rkm 13 closest to the time of initiation of migration (15-min intervals). Mean daily temperature was calculated for the 24-h day upon initiation of upriver migration at rkm 13 (midnight to midnight). Changes in river temperatures were quantified using the number of 1-d sequential periods of declining or inclining mean daily river temperature at rkm 13, with a minimum trend of 1 d. This approach allowed a 1-d inclining trend to interrupt an overall multiday period of declining temperature or vice versa. If mean daily temperature did not change from one day to the next, the neutral day was counted towards the preceding temperature period. If a fish initiated upriver migration before the daily maximum of a day that marked a change in trends in mean daily temperatures, that day was assigned to the subsequent period. Slopes during periods of declining or inclining mean daily water temperature were calculated using simple linear regression.

Logistic regression was used to test for a threshold effect in the probability of initiation of upriver migration (categorical dependent variable) as a function of mean daily water temperature (independent continuous variable). From the day of tagging until the day of initiation of upriver migration past rkm 7, each day for each fish was assigned a binomial value (1 and 0) of moving or holding with the associated mean daily water temperature to 0.1°C. The day of tagging and the day of upriver migration initiation were assigned to moving, whereas the days in between were assigned to holding.

After initiation of upriver migration by tagged Chinook salmon, use of en route thermal refuges was determined to the nearest hour by comparison of ambient river temperature with body temperature. Biotelemetry data were used to determine the location of the refuge. Thermal refuge use was defined as a decrease in the expected diurnal pattern of body temperature greater than 1°C for at least 1 h. In the absence of body temperature data, biotelemetry data were examined for obvious delays in the vicinity of known thermal refuges, with the associated delay assumed to be the maximum possible duration of thermal refuge use. For consistency with relevant published research (Goniea et al. 2006), substantial thermal refuge use was defined as fish presence for at least 12 h. Whether or not substantial en route thermal refuge use significantly decreased mean travel rates was determined by comparing (1) mean travel rates with delays at refuges included versus (2) mean travel rates with delays at refuges excluded. Specifically, a first grouping was created by assigning a ranking to each fish from highest to lowest based on their travel rates, while a second grouping was created by repeating that procedure with any delays from substantial thermal refuge use. These two groups were then compared for significant differences using the Mann–Whitney nonparametric test statistic U following the ranking procedure protocols described by Zar (1999). This ranking procedure was also used to test for significant differences in travel rates between years both with and without exclusion of refuge delays.

Thermal experience was evaluated using archival body temperature records from 2004 and 2005. Mean weekly, mean maximum daily, and mean minimum daily body temperatures were calculated for the first and second weeks (1 week = 168 h) of upriver migration. These metrics were chosen for consistency with common numeric temperature criteria for salmonids (Richter and Kolmes 2005). The Mann–Whitney ranking procedure was also used to test for significant differences between years and between weeks for each metric. The acclimation period was defined as extending from the fish's time of tagging to the fish's final initiation of upriver migration, with mean, maximum, and minimum body temperatures calculated from archival body temperature records. If a fish moved from the ocean to the estuarine salt wedge for a substantial portion of this period, only body temperatures from estuary residence were used to calculate acclimation temperature metrics. The distinct thermal signatures of the ocean versus the estuary allowed for

TABLE 1.—Summary of tagging information and fates of relevant adult Chinook salmon tagged during 2004 and 2005 at the mouth of the Klamath River at river kilometer (rkm) 0. Mean daily temperature (MDT) is reported for the day of tagging in the Klamath River main stem at rkm 13. Archival tags (iButtons [iB]) recorded body temperature. Fish number 149.413 was the first fish tagged since 14 June 2004 (with continual effort), and fish number 137 was the first fish tagged in 2005 (no effort before that date). The term "spawned" indicates that the fish was found in a spawned-out condition (FL = fork length; IGH = Iron Gate Hatchery; TRH = Trinity River Hatchery; na = not available).

Tagging year	Tag code	Tagging date	MDT (°C)	FL (cm)	Run (river, season)	Sex	iB recovery	Fate or last observation[a]
2004	149.413	9 Jul	20.8	83	Trinity, summer	na	Yes	TRH, rkm 252, 30 Sep
	149.722	15 Jul	21.3	65	Trinity, summer	na	No	TRH, rkm 252, 4 Oct
	149.743	15 Jul	21.3	74	Trinity, summer	na	Yes	Caught, rkm 90, Trinity River, 6 Aug
	149.114	21 Jul	23.0	84	Trinity, summer	na	No	rkm 70, Trinity River, 28 Aug
	149.392	22 Jul	23.5	72	Trinity, summer	na	Yes	Caught, rkm 86, Trinity River, 7 Aug
	149.494	26 Jul	24.4	85	Trinity, summer	na	Yes	Spawned, rkm 207, Trinity River, 22 Oct
	149.515	26 Jul	24.4	75	Trinity, summer	na	Yes	Spawned, rkm 231, Trinity River, 3 Nov
	149.714	19 Aug	23.2	78	Klamath, fall	Male	Yes	IGH, rkm 310, 11 Oct
2005	137	1 Aug	23.3	74	Trinity, summer	na	No	Trinity River, rkm 71, 20 Aug
	138	3 Aug	23.8	73	Trinity, summer	na	Yes	Caught, rkm 50, Klamath River, 7 Aug
	140	10 Aug	24.0	84	Trinity, summer	Female	Yes	Spawned, rkm 206, Trinity River, 14 Oct
	143	10 Aug	24.0	70	Trinity, summer	Female	Yes	Caught, rkm 242, Trinity River, 22 Sep
	144	10 Aug	24.0	71	Trinity, summer	na	No	rkm 70, Trinity River, 14 Aug
	145	11 Aug	23.5	75	Trinity, summer	na	No	TRH, rkm 252, 17 Oct
	146	11 Aug	23.5	67	Klamath, fall	na	No	IGH, rkm 310, 26 Sep
	147	11 Aug	23.5	73	Trinity, summer	na	No	TRH, rkm 252, 30 Sep
	150	12 Aug	23.2	77	Trinity, summer	Male	Yes	TRH, rkm 252, 26 Sep
	155	18 Aug	23.0	83	Trinity, summer	na	No	TRH, rkm 252, 1 Oct

[a] Rkm reported as measured from the mouth of the Klamath River.

an indirect determination of general fish location during the acclimation period from archival body temperature records in 2004. In 2005, fish location was determined directly by biotelemetry data.

Results

Eighteen adult Chinook salmon did not meet either of the exclusion criteria and provided sufficient telemetry records to evaluate behavioral responses to high water temperatures and changes in environmental variables. Of these 18 fish, 8 were tagged in July and August 2004 and 10 were tagged in August 2005 (Table 1). Based on their destinations and coded wire tag records from harvested cohorts, all of these fish were considered Trinity River spring-run fish (stream type; Healey 1983) except for two early migrating Klamath River fall-run fish (ocean type). Of the 18 fish, 12 successfully migrated to spawning grounds or hatcheries. Of the remaining six fish, four were harvested in the lower Klamath River and two were last observed at the confluence of the Trinity River (rkm 70). There was no evidence of disease-related mortality among the 18 fish. Ten of the 18 archival temperature tags were recovered, seven of which were from fish that reached spawning grounds or hatcheries.

After tagging and before initiation of upriver migration, all fish held in the cold salt wedge of the Klamath River estuary, returned to the ocean, or used both environments. Residence times in the estuary and ocean ranged from 13 to 667 h (mean ± SE = 247.2 ± 43.2 h, SD = 184.8 h, $n = 18$). Based on available records, mean thermal experience (thermal acclimation history) during these periods ranged from 11.2°C to 18.5°C (mean = 15.0 ± 0.83°C, SD = 2.6°C, $n = 10$; Table 2).

Initiation of upriver migration by adult Chinook salmon was compared in 2004 (Figure 2) and 2005 (Figure 3) relative to water temperatures, flow volume, and light intensity. River discharges reflected atypical pulsed releases of water from Trinity Dam in late August and September 2004 and from Iron Gate Dam in late August 2005. No measurable precipitation or substantial drops in atmospheric pressure were associated with initiation or resumption of upriver migration by tagged Chinook salmon (Figure 4). Dissolved oxygen levels remained well above 5 mg/L during the study period in both years, and there were no unusual decreases in dissolved oxygen levels associated with partial or complete migration blockages (Figure 5). Mean daily river temperatures at rkm 13 upon initiation of upriver migration ranged from 21.8°C to 24.0°C (mean ± SE = 22.9 ± 0.13°C, SD = 0.6°C, $n = 20$). Logistic regression analysis showed no significant relationship between probability of moving as a function of mean daily temperature ($P > 0.05$, $n = 210$ [38 moving + 172 holding]). Additional filtering of data (e.g., excluding all but the day before and the day of resumed migration) also did not produce significant relationships between the probability of moving and mean daily river tempera-

TABLE 2.—Thermal histories (mean, maximum, and minimum temperatures) during the acclimation period for adult Chinook salmon tagged in 2004 and 2005 ($n = 10$; F = fall-run fish). The acclimation period is defined as the period after tagging at river kilometer (rkm) 0 on the Klamath River and before initiation of upriver migration above the estuary (passage past rkm 7). The residence period is the total amount of time spent between tagging and initiation of upriver migration (p indicates that ocean residency was followed by an extended period of estuary residency, in which case the ocean thermal record was omitted). Date is the day of passage above the estuary at rkm 7, and environment designates whether the acclimation history primarily occurred while fish were in the estuary, ocean, or either.

Tagging year	Tag code	Mean (°C)	Maximum (°C)	Minimum (°C)	Residence period (h)	Date	Environment
2004	149.413	18.5	22.0	15.3	248p	1 Aug	Estuary
	149.743	14.4	21.4	8.5	447	2 Aug	Either
	149.392	13.6	19.3	13.6	282	3 Aug	Either
	149.494	17.9	24.1	14.4	246	5 Aug	Either
	149.515	17.4	20.8	15.1	110	2 Aug	Either
	149.714F	16.8	22.8	14.0	13	21 Aug	Either
2005	150	14.2	20.7	11.1	95	16 Aug	Ocean
	143	11.2	21.5	8.7	154	16 Aug	Ocean
	140	11.2	21.5	8.7	296	22 Aug	Ocean
	138	14.3	19.9	11.7	37	5 Aug	Ocean
Mean		15.0	21.4	12.1			
SE		0.83	0.44	0.86			
SD		2.6	1.4	2.7			

ture. With the exception of fish number 138, all fish initiated migration in association with periods of declining mean daily river temperature but not necessarily at the beginning of a given trend (Figures 2, 3). Chinook salmon usually initiated migration during a major decline in mean daily river temperature (>2°C change in mean daily temperature over the period of trend), but some fish migrated after smaller decreases in river temperature. Whether river temperatures were increasing or decreasing influenced migration inhibition. Migration was inhibited at lower mean daily river temperatures during periods of increasing river temperature than during periods of declining river temperature (e.g., fish number 149.114). Fish did not initiate migration during periods of inclining mean daily river temperature as short as 1 d during an otherwise major period of declining temperature (e.g., 4 August 2004). Once upriver migration was initiated, movement was generally rapid and uninterrupted.

During the first week (168 h) of migration, mean body temperatures (equivalent to the mean weekly average temperature [MWAT]) ranged from 21.3°C to 22.6°C (mean = 21.9 ± 0.20°C, SD = 0.6°C, $n = 7$), mean minimum daily body temperature (MWMnT) ranged from 19.8°C to 21.1°C (mean = 20.6 ± 0.21°C, SD = 0.66°C, $n = 7$), and mean maximum daily body temperature (MWMT) ranged from 22.2°C to 23.8°C (mean = 23.1 ± 0.25°C, SD = 0.7°C, $n = 7$; Table 3). Maximum body temperatures during the first week ranged from 23.8°C to 25.6°C (mean = 24.4 ± 0.16°C, SD = 0.6°C, $n = 10$). Mann–Whitney nonparametric ranking tests showed no significant difference between mean weekly body temperatures in 2004 versus 2005 during the first week of migration (Mann–Whitney $U_{0.05(2),3,4}$; MWAT, $P = 0.20$).

During the second week of migration, mean body temperatures experienced by migrating Chinook salmon began to decrease as the fish continued upriver and all metrics were significantly less compared with those observed during the first week ($U_{0.05(1),7,7}$; MWAT, $P = 0.0005$; MWMT, $P = 0.0005$; MWMnT, $P = 0.00175$). Mean body temperatures ranged from 17.0°C to 20.8°C (mean = 19.4 ± 0.59°C, SD = 1.6°C, $n = 7$), MWMnTs ranged from 15.1°C to 20.0°C (mean = 18.0 ± 0.73°C, SD = 1.9°C, $n = 7$), and MWMTs ranged from 18.7°C to 21.7°C (mean = 20.7 ± 0.48°C, SD = 1.3°C, $n = 7$; Table 4). No significant difference between mean weekly body temperatures in 2004 versus 2005 was evident during the second week of migration ($U_{0.05(2),3,4}$; MWAT, $P = 0.20$). Mean fish body temperatures during the estuarine–marine acclimation period, upon initiation of upriver migration, and during the first and second weeks of upriver migration are compared in Figure 6.

Use of en route thermal refuge habitats for at least 1 h was displayed by 67% of the tagged Chinook salmon. Fish residence in these habitats was not usually extensive, however; the percentage of fish residing for 12 h or longer was 33% in 2005 and 0% in 2004 (Table 5). While fish were residing in en route thermal refuge habitats, body temperatures decreased over ambient temperature by up to approximately 4.5°C. No tagged Chinook salmon were observed using more than one refuge. The Blue Creek thermal refuge was the most frequently used en route habitat, representing

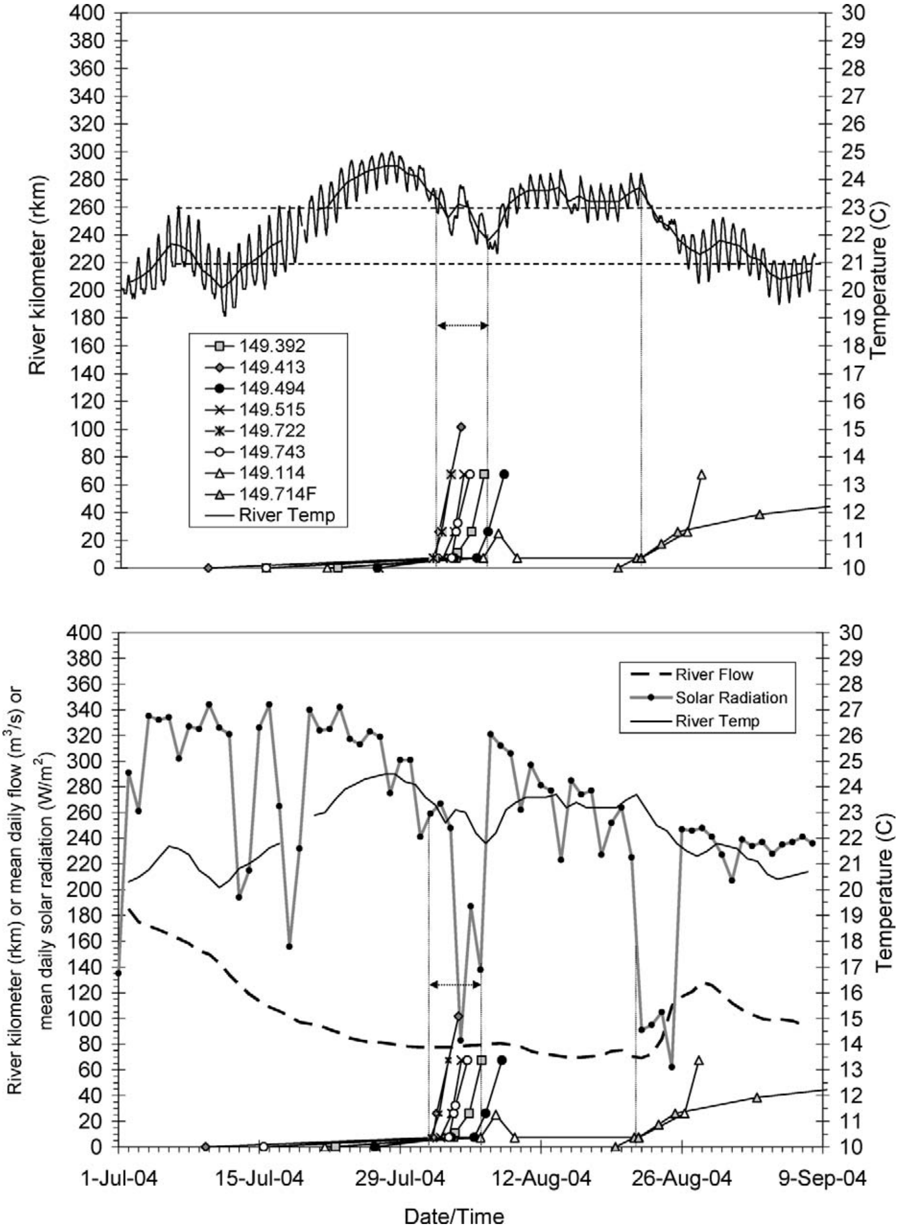

FIGURE 2.—Migratory movements in the Klamath River (from tagging at river kilometer [rkm] 0 to rkm 70 or the nearest observation) for eight adult Chinook salmon (individuals are represented by codes beginning with "149"; F = fall-run fish) tagged in 2004 in relation to Klamath River water temperatures at rkm 13 (upper panel; 15-min intervals or center line for mean daily); the temperatures at which individuals resumed upriver migration and the importance of declining water temperature trends are shown. The upper thermal limit of 23°C (mean daily temperature) measured in this study is highlighted by the horizontal dashed line in comparison with the 21°C value typically reported in literature reviews. Movement in relation to mean daily flow at rkm 13 (lower panel; large dashed line) and average daily solar radiation (gray line with black circles) illustrates (1) the lack of a consistent relationship between fish movements and river discharge and (2) the decrease in solar radiation that typically preceded a declining trend in river temperature associated with resumption of upriver migration. Vertical lines designate initiation of upriver migration past the estuary at rkm 7. A pulsed flow released from Trinity Dam resulted in the flow increase in late August–early September 2004.

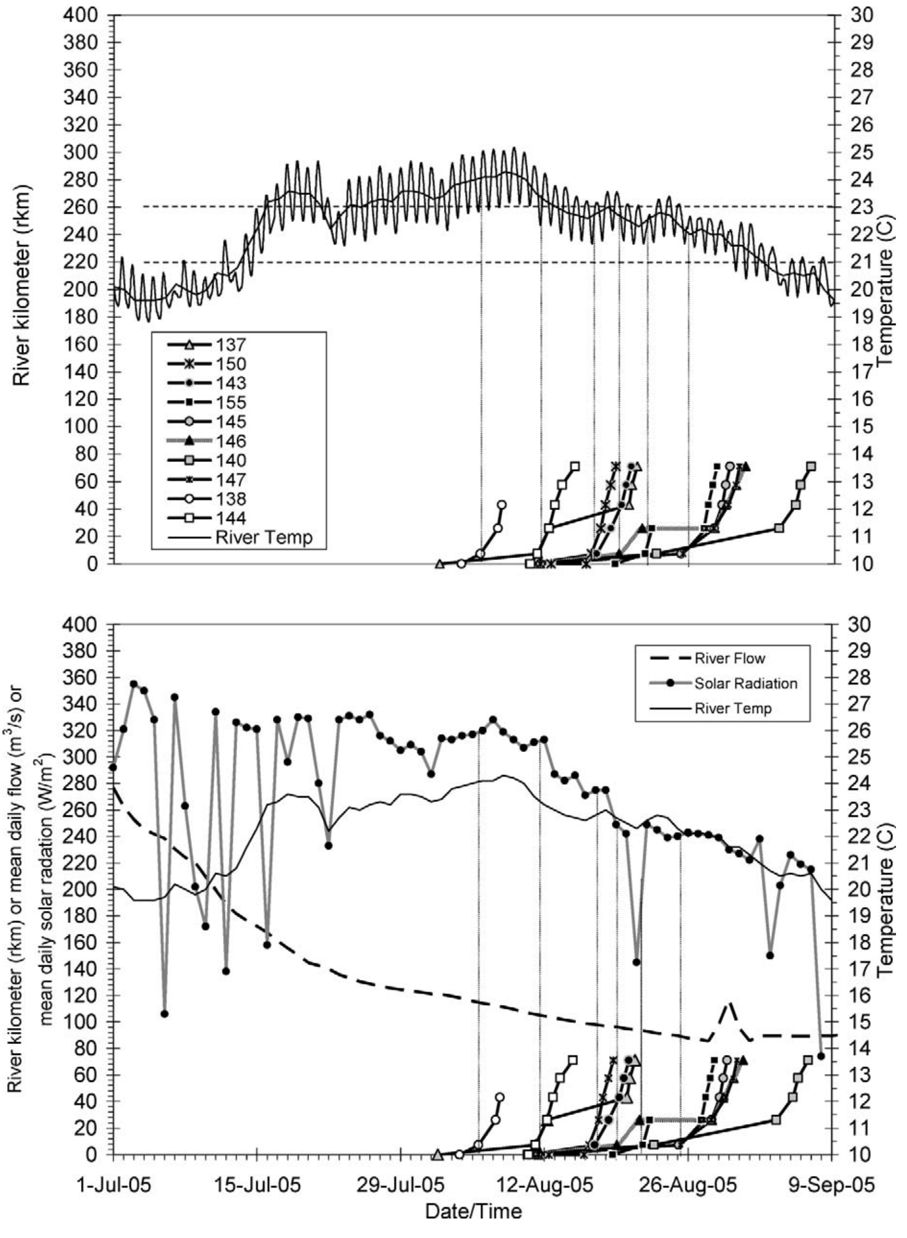

FIGURE 3.—Migratory movements in the Klamath River (from tagging at river kilometer [rkm] 0 to rkm 70 or the nearest observation) for ten adult Chinook salmon (individuals are represented by three-numeral codes; fish 146 = fall-run individual) tagged in 2005 in relation to Klamath River water temperatures at rkm 13 (upper panel; 15-min intervals or center line for mean daily); the temperatures at which individuals resumed upriver migration and the importance of declining water temperature trends are shown. The upper thermal limit of 23°C (mean daily temperature) measured in this study is highlighted by the horizontal dashed line in comparison with the 21°C value typically reported in literature reviews. Movement in relation to mean daily flow at rkm 13 (lower panel; large dashed line) and average daily solar radiation (gray line with black circles) illustrates (1) the lack of a consistent relationship between fish movements and river discharge and (2) the decrease in solar radiation that typically preceded a declining trend in river temperature associated with resumption of upriver migration. Vertical lines designate initiation of upriver migration past the estuary at rkm 7. A pulsed flow released from Iron Gate Dam resulted in the increased flow during late August 2005.

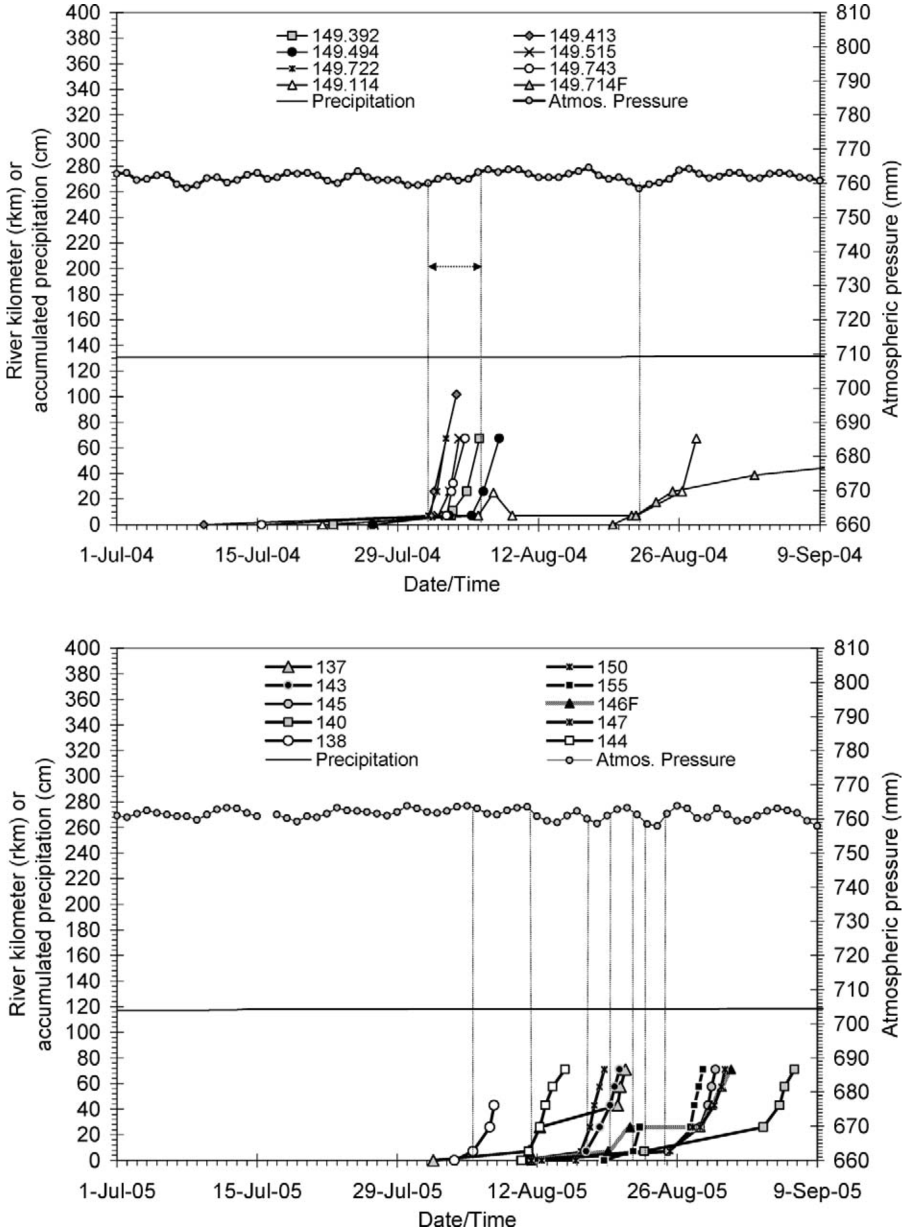

FIGURE 4.—Migratory movements in the Klamath River (from tagging at river kilometer [rkm] 0 to arrival near rkm 70 or the nearest observation) for adult Chinook salmon tagged in 2004 (upper panel; $n = 8$; F = fall run) and 2005 (lower panel; $n = 10$) in relation to accumulated precipitation (cm) measured at rkm 95 and mean daily atmospheric pressure (mm) measured near rkm 250 on the Trinity River. The pattern illustrates the lack of a correspondence between fish movements and environmental variables potentially associated with weather fronts that produced periods of declining river temperature. Vertical lines designate initiation of upriver migration past the estuary at rkm 7.

100% of the substantial refuge use ($\geq$ 12 h) and 67% of the total en route refuge use.

Within the lower Klamath River between the upper terminus of the estuary (rkm 7) and the confluence with the Trinity River (rkm 70), tagged Chinook salmon migration rates were moderately fast (mean = 21.4 km/d, maximum = 46.4 km/d; Table 5). Migration rates depended on the extent of thermal refuge use, year, and

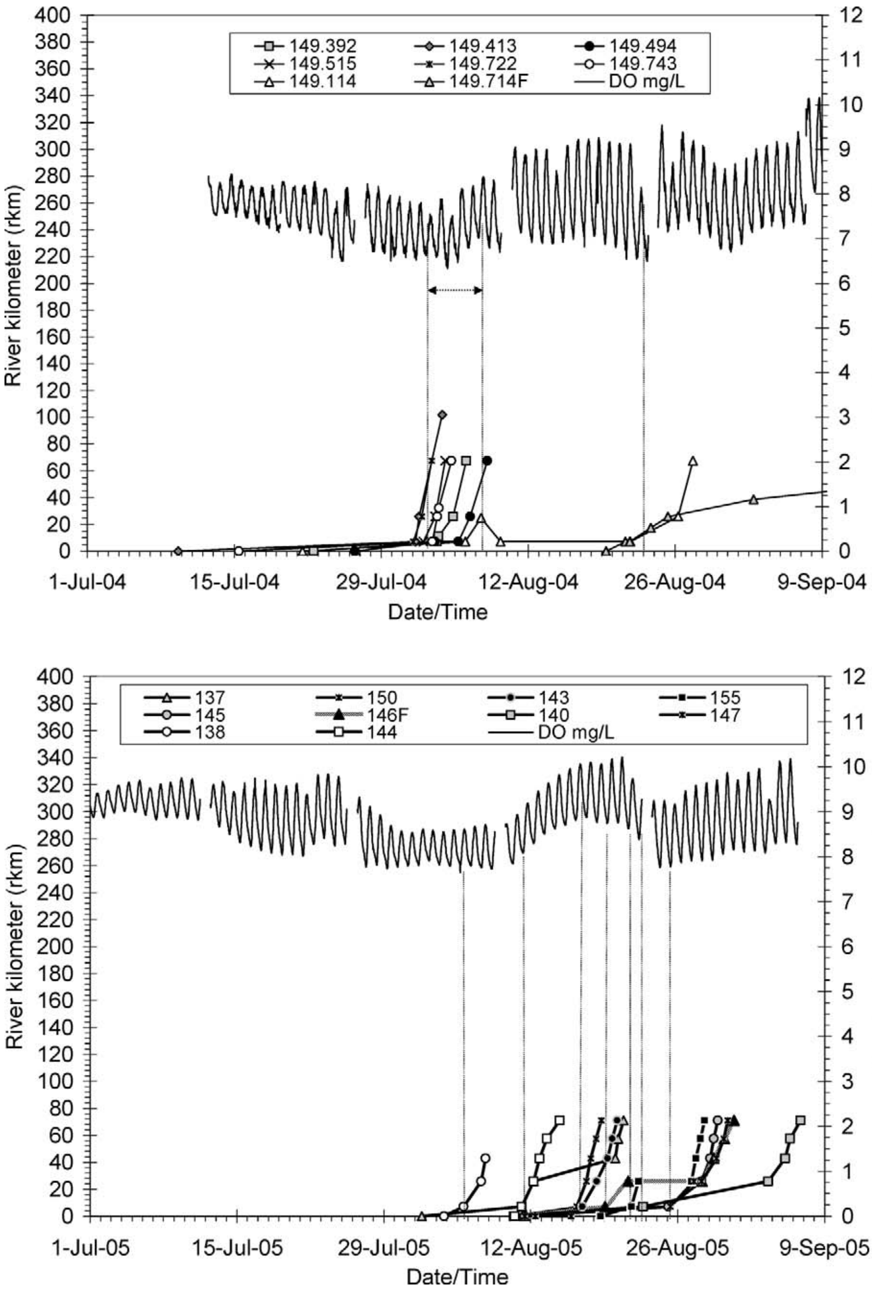

FIGURE 5.—Migratory movements in the Klamath River (from tagging at river kilometer [rkm] 0 to arrival near rkm 70 or the nearest observation) for adult Chinook salmon tagged in 2004 (upper panel; $n = 8$; F = fall run) and 2005 (lower panel; $n = 10$) in relation to dissolved oxygen (DO; mg/L) measured at rkm 13, illustrating the lack of migration inhibition due to low dissolved oxygen. Vertical dotted lines designate initiation of upriver migration past rkm 7.

run group. For example, tagged Chinook salmon that used a thermal refuge for 12 h or more had significantly slower migration rates ($U_{0.05(1),4,14}$; $P = 0.0075$) than fish that did not. However, after excluding the time spent in refuges, there was no significant difference in migration rates ($U_{0.05(2),4,14}$; $P > 0.20$). Migration rates were significantly slower in 2005 than in 2004, both with ($U_{0.05(1),4,14}$; $P > 0.025$) and without ($U_{0.05(1),4,14}$;

TABLE 3.—Body temperatures (°C) of archival-tagged adult Chinook salmon during the first week of upriver migration in the Klamath River basin. Body temperatures were measured in 60–120-min intervals (F = fall-run fish; MWAT = mean weekly average body temperature; MWMT = mean weekly average of the maximum daily body temperature; MWMnT = mean weekly average of the minimum daily body temperature). Date refers to the day at the end of the first week, with corresponding fish location on that day (river kilometer [rkm]).

Tagging year	Tag code	MWAT (range)	MWMT	MWMnT	Date	rkm
2004	149.413	21.3 (24.4–18.0)	22.4	19.8	8 Aug	146
	149.494	22.3 (24.8–18.1)	23.5	20.6	12 Aug	120
	149.515	21.4 (24.8–18.4)	22.6	19.8	9 Aug	156
	149.714F	21.4 (23.8–19.6)	22.2	20.6	28 Aug	30
2005	150	22.6 (24.3–20.3)	23.8	21.1	23 Aug	133
	143	22.5 (24.4–20.3)	23.8	21.1	23 Aug	120
	140	22.1 (23.8–20.4)	23.2	20.9	29 Aug	17
Mean		21.9	23.1	20.6		
SE		0.20	0.25	0.21		
SD		0.6	0.7	0.6		

$P > 0.005$) exclusion of refuge use greater than 12 h; this result was possibly due to differences in river temperature and flow between years. The two fall-run Chinook salmon (fish numbers 149.714F and 146F) had the slowest and third-slowest migration rates of all 18 monitored individuals. This observation was consistent with the slow migration rates observed among other tagged fall-run Chinook salmon in the lower Klamath River between 2003 and 2006 (author's unpublished biotelemetry data).

Discussion

To determine the upper thermal limits to migration in adult Chinook salmon, it is advisable to compare behavioral responses of fish at differing durations of thermal exposure. At the shortest duration, records of the maximum body temperatures experienced by adult Chinook salmon migrating in the Klamath River basin during the summer and fall months of 2004 and 2005 ranged from 23.8°C to 25.6°C (mean = 24.4°C). At a slightly longer time scale, the 24-h diel river temperature cycle can be represented by the daily mean, which is one of several possible single metrics that are applicable to behavioral responses at an acute temporal scale. At the initiation of the upriver migration by adult Chinook salmon after a period of thermal migration inhibition, mean daily river temperatures ranged from 21.8°C to 24.0°C (mean = 22.9°C). Since exposure to lethal water temperatures is cumulative (DeHart 1975, as cited in McCullough et al. 2001), it follows that weekly (168 h) temperature metrics are more appropriate indicators of behavioral response and physiological capacity at a chronic temporal scale than are daily metrics. The MWATs of adult Chinook salmon ranged from 21.3°C to 22.6°C (mean = 21.9°C), and MWMTs ranged from 22.2°C to 23.8°C (mean = 23.1°C). The highest values in all ranges demonstrate the ultimate upper ability of individuals within a population to migrate in the face of extremely high water temperatures. Use of mean temperature values to determine the upper thermal limit to migration is more appropriate as a single metric, in part because it

TABLE 4.—Body temperatures (°C) of archival-tagged adult Chinook salmon during the second week of upriver migration in the Klamath River basin. Body temperatures were measured in 60–120-min intervals (F = fall-run fish; MWAT = mean weekly average body temperature; MWMT = mean weekly average of the maximum daily body temperature; MWMnT = mean weekly average of the minimum daily body temperature). Date refers to the day at the end of the second week, with corresponding fish location on that day (river kilometer [rkm]).

Tagging year	Fish	MWAT (range)	MWMT	MWMnT	Date	rkm
2004	149.413	17.0 (20.6–14.8)	18.7	15.1	15 Aug	172
	149.494	20.8 (23.0–18.3)	22.1	19.3	19 Aug	160
	149.515	17.6 (22.9–14.5)	19.6	15.6	16 Aug	194
	149.714F	20.6 (22.1–18.9)	21.7	20.0	4 Sep	42
2005	150	19.1 (22.4–11.9)	20.6	18.1	30 Aug	192
	143	19.8 (21.8–14.8)	20.5	18.6	30 Aug	140
	140	20.8 (22.5–18.3)	21.9	19.5	5 Sep	57.5
Mean		19.4	20.7	18.0		
SE		0.59	0.48	0.73		
SD		1.6	1.3	1.9		

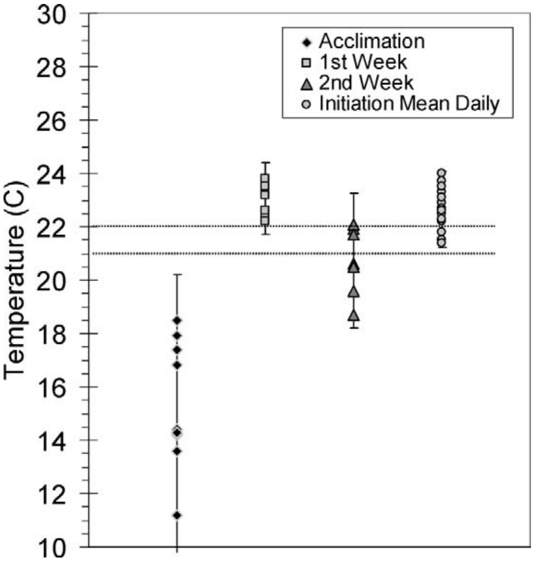

FIGURE 6.—Mean (±2SD) daily river temperature in the Klamath River (river kilometer 13) during the day of initiation of upriver migration ($n = 20$) plus mean body temperatures for archival-tagged adult Chinook salmon before the initiation of upriver migration (acclimation period = 13–447 h, $n = 10$), during the first week (168 h) of upriver migration (168 h, $n = 7$; <168 h, $n = 3$), and during the second week of upriver migration ($n = 7$) for all available body temperature records from 2004 and 2005. The horizontal dotted lines designate the upper incipient lethal temperatures for adult Chinook salmon (from Coutant 1970).

averages variation among individuals, thereby reducing the influence of any outliers or potential instrument errors. Based on these considerations, I propose that the upper thermal limits to migration for adult Chinook salmon in the Klamath River basin are a mean daily temperature of 23°C, a corresponding mean weekly temperature of 22°C, and a mean weekly maximum temperature of 23°C. Temperatures above these values appear to completely block migration in almost all circumstances. The only exceptions observed have involved fish retreating downstream to seek thermal refuges or fish that are exceptionally late in their migratory progression. These conclusions are strengthened by the fact that tagged Chinook salmon migrated past accessible thermal refuges without stopping, which precludes the possibility that the fish were forced to continue migrating upriver at temperatures beyond their normal thermal limit in the absence of a thermal refuge.

The upper thermal limits to adult Chinook salmon migration as measured by the results from this study are substantially higher than previously reported in the literature. After reviewing all pertinent research, McCullough (1999: 75) concluded that "...a water temperature of 21°C represents the upper migration limit for all races" of Chinook salmon. Subsequent reviews by McCullough et al. (2001) and Richter and Kolmes (2005) concurred with McCullough's (1999) conclusion of a 21°C limit. Potential differences in fish physiological responses and costs between instantaneous temperatures of 21°C and mean daily temperatures of 23°C could be substantial. Based on these differences, it is possible that Chinook salmon in the high thermal regime of the Klamath River basin have evolved higher thermal tolerances than other stocks, which has been previously speculated by researchers with the basin as noted by Bartholow (1995). However, the weight of evidence in the literature has not demonstrated the evolution of significant stock-specific thermal tolerances within species of salmonids (e.g., Sonski 1984; Konecki et al. 1995a, 1995b).

A cursory examination of all relevant studies of thermal blocks to migration among adult Chinook salmon suggests that the high upper thermal limits to migration measured in this study using Klamath River basin Chinook salmon might not be applicable to other river systems (Hallock et al. 1970; Stuehrenberg et al. 1978; Stabler et al. 1982; Alabaster 1988, 1989; Bumgarner et al. 1997; Fresh et al. 1999; Goniea et al. 2006). However, a more thorough review suggests that differences in the upper thermal limits between stocks of adult Chinook salmon are probably not as great as they first appear due to differences in study methods, data analysis, and thermal regimes between study river systems. For example, none of the previous studies reported water temperatures with sufficient detail to allow proper comparisons, and data on water temperatures for the entire migration period in each year (i.e., to illuminate the broader context) were not provided. Other problems were that publications (1) did not contain the supporting data they were purported to provide (Fish and Hanavan 1948), (2) had insufficient sample size ($n = 2$; Bumgarner et al. 1997), (3) lacked accounting for obvious confounding variables, such as low dissolved oxygen concentrations (<5 mg/L; Hallock et al. 1970), and (4) varied in the definition of thermal blocks as partial (Stuehrenberg et al. 1978; Goniea et al. 2006) versus complete (Alabaster 1988, 1989). Finally, none of these studies measured actual salmon body temperatures. Considering all of the problems listed, the range in reported values (18.9–22.4°C) may not accurately characterize the upper thermal limits to migration in adult Chinook salmon. The high upper thermal limits to migration measured for adult Chinook salmon in the Klamath River basin may not be without precedent, which

TABLE 5.—Adult Chinook salmon migration rates in the lower Klamath River from the upper terminus of the estuary (river kilometer [rkm] 7) to the Trinity River confluence (near rkm 70) with and without the period of time spent at en route thermal refuges (F = fall-run fish; na = not available). Fish number 138 was the only fish that did not arrive at rkm 70 (caught at rkm 50). Refuge durations with asterisks denote inference from biotelemetry data only. For refuge locations, "LT Cr." refers to a creek confluence with the lower Trinity River (below rkm 140); "LK Cr." refers to a creek confluence with the lower Klamath River (below rkm 70); and "Blue Cr." refers to the Klamath River confluence with Blue Creek at rkm 26. The mean, SE, and SD for travel rates without refuge use were calculated using data from all 18 fish but substituting the travel rate with the duration of refuge residence excluded for the four fish that used refuges for more than 12 h.

		Travel rate (km/d)			
Tagging year	Tag code	With refuge use	Without refuge use	Refuge use (h)	Refuge location
2004	149.413	37.3	na	0	na
	149.722	46.4	na	0*	na
	149.743	29.3	na	10	LT Cr.
	149.114	29.4	na	0*	na
	149.392	37.0	na	1	LT Cr.
	149.494	25.9	na	10	LT Cr.
	149.515	45.7	na	1	Blue Cr.
	149.714F	3.7	na	1	Blue Cr.
2005	137	32.0	6.6	<187*	LK Cr.
	138	17.2	na	3	Blue Cr.
	144	17.5	na	0*	na
	143	19.0	na	6	Blue Cr.
	140	4.2	na	0	na
	146F	12.2	5.2	169*	Blue Cr.
	145	13.5	na	0*	na
	147	13.4	11.7	<17*	Blue Cr.
	150	27.2	na	1	Blue Cr.
	155	33.1	9.1	121*	Blue Cr.
Mean		24.7	21.4		
SE		3.0	3.3		
SD		12.9	14.0		

potentially weakens the argument for stock-specific thermal tolerances in terms of migration ability.

Analysis of adult Chinook salmon responses to high water temperatures in the Klamath River basin at a broad temporal scale also revealed the influence of changing trends in water temperatures, which does not appear to have been previously reported in the literature. The lack of a significant logistic regression relationship between the probability of moving versus holding as a function of mean daily water temperature is most likely explained by the confounding variable of whether water temperatures were rising or falling in association with synoptic-scale weather fronts. A range of equivalent water temperatures can produce different responses among adult Chinook salmon due to the influence of temperature trends. With one exception, all Chinook salmon initiated upriver migration in association with periods of declining river temperature. Periods of rising mean daily river temperature as short as 1 d seemed sufficient to prevent the initiation of migration. Errors in judging thermal windows of migratory opportunity by adult Chinook salmon would probably lead to increased thermal exposure and migration delays, thereby leading to increased risk of reduced reproductive fitness or premature death (Hyatt et al. 2003; Naughton et al. 2005). The ability of adult Chinook salmon to correctly gauge the onset of periods of declining or inclining river temperature appears to be a vital mechanism for taking advantage of brief thermal windows for upriver migration.

Periods of major declines in river temperature during summer 2004 and 2005 in the Klamath River basin were preceded by reductions in air temperature and solar radiation associated with synoptic-scale weather fronts. This observation conforms to known principles of river temperature dynamics (Sinokort and Stefan 1993). Besides water temperature, potential variables used by adult Chinook salmon to gauge the onset of periods of declining water temperature logically should be associated with weather fronts. Potential variables that were plausibly detectable by Chinook salmon included increasing precipitation or an associated increase in river discharge, decreasing atmospheric pressure, or decreasing light intensity. There was no correspondence between the initiation of upriver migration by adult Chinook salmon and changes in river discharge (stable or decreasing), precipitation (none), or atmospheric pressure (negligible and inconsistent changes). However, declining light intensity as measured by mean daily solar radiation did correspond to the initiation of upriver migration by adult Chinook salmon. The sensitivity of salmon to changes in light levels has been previously documented with the correlation of seasonal migrations to photoperiod (Eriksson et al. 1982; Healey 1991). The apparent use of light intensity on a daily basis by adult Chinook salmon in this study to assist in gauging the onset of declining river temperature is probably unprecedented, although barometric pressure has been significantly correlated with adult Chinook salmon movements in other settings (Allen 1959).

Integral to the successful use of typically brief thermal windows for migration is the ability to migrate upriver rapidly. However, rapid upriver migration can only work if habitat with a suitable thermal regime is available within an appropriate distance in space or time, thereby limiting stressfully high temperature exposures to tolerable levels. It is important to note that the thermal inertia of body mass has a limited ability to insulate poikilothermic fish from high water temperatures as demonstrated experimentally by Berman (1990), who determined that the internal body temperature of adult Chinook salmon equilibrated to a warm water bath within approximately 1 h depending on the size of the fish. The swimming distance achievable by an adult salmon in 1 h is relatively limited compared with the distances often involved in freshwater migration. For example, spring-run Chinook salmon bound for the Trinity River encounter a declining longitudinal temperature profile as they migrate upriver beginning around rkm 120 (as measured from the mouth of the Klamath River). By approximately rkm 185, river temperatures have cooled enough to provide suitable prespawn holding habitat. The declining longitudinal temperature profile encountered as Chinook salmon migrate up the Trinity River is a function of the proximity to Trinity Dam and its cold (i.e., 9°C) hypolimnetic releases. The resulting thermal envelope, essentially a 70-km-long thermal refuge within a moderate 185-km swimming distance of the Pacific Ocean, is a necessary feature that allows the Trinity River to support stream-type Chinook salmon with summer run timing (i.e., July and August). In contrast to the Trinity River, the main-stem Klamath River currently has no reach- or segment-scale thermal refuge downstream from Iron Gate Dam (at rkm 310), and coolwater tributaries become progressively smaller and less frequent as the Chinook salmon migrate upriver. Before the construction of Klamath River main-stem dams that blocked access to large thermal refuges, there were apparently populations of stream-type Chinook salmon that migrated above the confluence of the Trinity River during the summer (Snyder 1931).

En route thermal refuge habitats at the confluences of cool tributaries, as opposed to reach- or segment-scale thermal refuges, appear to serve a vital role in providing emergency relief from excessively high water temperatures for a relatively small but important portion of migrating adult Chinook salmon within the Klamath River basin. The use of thermal refuges by salmonids has been documented by numerous researchers, including for adult Chinook salmon during migration (Stuehrenberg et al. 1978; Goniea et al. 2006) and during the prespawn holding period (Berman and Quinn 1991; Torgersen et al. 1999). After analyzing thermal refuge use by spring Chinook salmon in the John Day River, Oregon, Torgersen et al. (1999) recommended using multiple spatial scales to evaluate the significance of thermal refuge use by fish. The differing spatial scales and functions of thermal refuge habitats in the Klamath River basin at cool tributary confluences versus larger main-stem reaches and segments support the recommendation by Torgersen et al. (1999).

The temperatures at which adult Chinook salmon in the Klamath River basin were observed actively migrating approached or exceeded the highest ultimate upper incipient lethal values determined for any life stage of this species (Brett 1952). This finding demonstrates that Chinook salmon adults are capable of enduring, at least for a limited time period, potentially lethal instantaneous temperatures while continuing to migrate. While there is certainly a limit to the duration of exposure that can be endured, it is significant that although temperatures during the first week of migration equaled or exceeded the upper incipient lethal temperature for adult Chinook salmon (Coutant 1970), tagged Klamath River basin adults still had high rates of success in reaching spawning grounds. Cumulative exposure to deleterious temperatures, however, can lead to delayed mortality after arrival on spawning grounds; therefore, when comparing results from the Klamath River basin to numeric water quality criteria, it is important to distinguish between tolerable versus optimal thermal conditions for migration.

While it is encouraging that tagged adult Chinook salmon in the Klamath River basin were able to successfully migrate to spawning grounds despite experiencing high body temperatures, no assessment was made of the actual spawning success rates or the sublethal effects on reproductive performance. Potential sublethal effects include decreased egg size and viability, reduced energy availability for mate selection and construction of redds, and impaired immune function (Ellis 1981; Cooke et al. 2006; Young et al. 2006). In most years within the Klamath River basin, a small percentage of migrating adult Chinook salmon perish en route due to causes unrelated to harvest or predation. However, limited data reveal that relatively high prespawn mortalities can occur on spawning grounds in some years and some locations. The high level of prespawn mortality highlights the importance of adequately monitoring spawning success rates to guard against undetected low spawning success even with high migration success, which would lead to overestimated spawner escapement. A typical numeric water temperature criterion for adult Chinook salmon migration is an MWAT of 14–16°C, which reflects optimal thermal conditions for migration as opposed to the tolerable but potentially costly thermal conditions reflected by the upper thermal limits to migration.

As future studies provide additional data on the upper thermal limits to migration for adult Chinook salmon, uncertainty in the variation of migratory ability at high water temperatures among adults from differing stocks and river basins should decrease. To improve comparability of studies from differing stocks and river basins, I recommend that future researchers (1) explicitly define the temperature metrics used and, if possible, provide metrics that evaluate acute (i.e., mean daily temperature) and chronic (i.e., MWAT and MWMT) temporal scales of fish response; (2) include water temperature graphs at sufficiently fine temporal resolution (i.e., hourly) and sufficiently broad duration (i.e., migration season) to provide proper context for fish behavior; (3) clearly differentiate between partial (at least some fish) versus complete (nearly all fish) blocks to migration and determine both if possible; and (4) make use of archival temperature devices to record fish body temperatures during tagging studies. Implementing these recommendations would also provide common metrics across studies, thereby allowing an examination of differences and similarities between stocks and river basins, the sublethal effects, and the associated bioenergetic implications. A broad but precise knowledge base on the effects of water temperature on adult Chinook salmon migration would facilitate efforts to accurately predict migratory responses in a changing environment and would assist in determining the consequences of migration at suboptimal temperatures.

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