Using Archival Tags to Infer Habitat Use of Central California Steelhead and Coho Salmon

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Abstract.—We deployed archival temperature loggers on juvenile and adult coho salmon *Oncorhynchus kisutch* and steelhead (anadromous rainbow trout) *O. mykiss* over both the freshwater and marine portions of their lifecycle in order to study their movements and thermal preferences. Beginning in 2003, loggers were deployed on juvenile coho salmon and juvenile and adult steelhead in a small central California coastal stream. A tag recovery from a coho salmon indicates the fish experienced variable temperatures on a daily to weekly basis in the marine environment (mean 13.3°C, range 10–18°C). Tags recovered from steelhead indicate use of a cooler, more stable, thermal habitat window in the marine environment (mean 11.0°C, range 8–14°C), often with little fluctuation over a period of weeks to months, and most thermal changes occurring at the seasonal time scale. Comparisons of steelhead data with sea surface temperature data suggest a northern migration out of the California Current to a narrow band of habitat that fluctuates between the southern boundary of the Bering Sea and north of the 40th parallel. In the shallow freshwater environment, steelhead appeared to be at the mercy of stream temperatures. However, in the estuary, where thermally variable habitats were available, steelhead used a surprisingly broad temperature range, including entering water thought to challenge their thermal tolerances (>20°C) even when cooler waters were available. Temperature loggers recovered on a local beach and island indicate tagged fish were consumed in the estuary by warm-blooded predators. All of these data coupled with a larger number of passive integrated transponder (PIT) tags, are helping to identify discrete habitats fish are using, exact dates of ocean entry and return, and enhance our understanding of marine survival and predation. Finally, archival tags may be useful in understanding habitat use of pelagic long-migrating species like steelhead, by tracking individuals in areas where other tagging technologies are poorly suited.

Introduction

What is known of the ocean distribution of salmon comes largely from commercial and research fisheries (Hartt and Dell 1986; Pearcy 1992). More recently, the results of tagging and marking studies have provided information on point to point locations and movements of individual fish (e.g., Myers et al. 1996; Weitkamp and Neely 2002). This information is biased to maturing or adult age classes due to the nature of gear types and the focus on adult fisheries. Therefore little information on early marine survival or habitat use of juveniles is available. Importantly, early marine habitat use may encompass a critical survival window (Pearcy 1992). Consolidating the above research with growing oceanographic data sets has provided insight into marine habitat use and distributions of Pacific salmon relative to oceanographic features (Burgner et al. 1992;

Welch et al. 1998b; Welch et al. 1998c). However, our understanding of the marine component still pales in comparison to the data available on the freshwater life history of salmonids.

Recent advances in electronic tag technology have resulted in tags small enough to be carried by salmonids and yet resilient to the stresses of the riverine and marine environments. This has resulted in two specific research directions: acoustic tags which emit an individual specific code that can be detected by receivers in riverine, estuarine and marine habitats (results reviewed extensively in this volume), and archival tags (or data storage tags) which collect data on the environmental conditions an individual fish encounters, some of which can be used to infer at-sea locations as well (Friedland et al. 2001; Hinke et al. 2005a; Hinke et al. 2005b; Reddin et al. 2006; Reddin et al. 2004; Walker et al. 2005; Walker et al. 2001; Walker et

al. 2000). Of course, tradeoffs exist between the two technologies. Acoustic tags can provide population-level estimates of survival and mortality past receiver arrays and fascinating insights into the life history (e.g., the detection of tagged individuals outside their previously expected home range), all without the need to recover the tags. On the other hand, these tags can only provide data where arrays are located, and detection rates are not 100%, resulting in potential biases of knowing only if fish passed a given receiver but nothing of their fate if undetected. Where acoustic arrays provide discrete temporal and spatial data points on multiple fish, archival tags have the advantage of providing continuous data of an individual's movements and habitat use throughout its migration. This of course comes with the necessity of recovering the tag and typically involves a bias of only having data from fish that were successful and survived long enough for the tag to be recovered. In addition, all tagging may be biased toward larger individuals in the population capable of carrying tags. Finally, tagged individuals could be more susceptible to complications associated with tagging that increase mortality or predation, especially acoustic tags which transmit in the ultrasonic frequency band used by many marine mammal predators.

For Pacific salmon populations along the California coast, most data on ocean distributions come from the recovery of coded wire tags (CWT) in ocean and research fisheries on coho *Oncorhynchus kisutch* and Chinook salmon *O. tshawytscha* and consist mostly of catch data for maturing adults (Weitkamp 2010; Weitkamp 2012, this volume; Weitkamp and Neely 2002). To date, almost no data exist on steelhead (anadromous rainbow trout) *O. mykiss* distributions in the California Current ecosystem, despite a much larger coastal breeding range than Chinook or coho salmon (Busby et al. 2000). Recent work by Hinke et al. (2005a, 2005b) used archival

tags recording temperature and depth data to study habitat use and distribution potential of subadult and adult Chinook salmon and found that these fish limited their ocean habitat use to a thermal band between 7.6 and 16°C, with 52% of the time spent between 9 and 12°C (Hinke et al. 2005b). Using this information and seasonal data on when tagged fish were known to be in the surface layer, they used sea surface temperature (SST) data from satellites to identify regions of the California Current with temperature ranges matching archival tag data to refine where a given fish was likely to have been. This provided varying precision of location, limited by times when fish were known to be using the surface layer and by the total surface area within the defined thermal limits. Despite lacking high resolution locations at all times, Hinke et al. (2005b) also determined how much surface habitat was available to Chinook salmon at any given time and how much that habitat varied between years, providing the potential for new insights between oceanographic data sets and Chinook salmon growth and survival. Similar work studying habitat use in the California Current ecosystem with archival tags has not been reported for steelhead or coho salmon to this point.

Due to higher densities of salmon stocks in northern Pacific latitudes, similar insights on thermal limits and distribution have been achieved through more traditional net and long-line surveys. In particular, sockeye salmon *O. nerka* have been shown to use a broader but ultimately cooler temperature window than Chinook salmon with ranges of 4–15°C, and seasonal periods rarely exceeding 7°C (Welch et al. 1998a). Their conforming distribution and areas of capture span the central Bering Sea, Japan to the west, Alaska to the east, and the 40th parallel to the south. Steelhead are found in a more restricted band of the North Pacific, both in terms of temperature and geography, with a northern limit south of the Alaskan coast, Bering Sea, and

Aleutian Islands, but a similar southern limit as sockeye salmon. Steelhead captures are reported from waters with a similar range of temperatures from about 5–15°C, but with less seasonal variation than sockeye and a central tendency that fluctuates between roughly 8 and 11°C (Burgner et al. 1992; Welch et al. 1998b). There are a few tag recoveries from northern California steelhead populations that suggest they are migrating to this same ocean region, but in general, data on this are lacking (Burgner et al. 1992; Myers et al. 1996).

Our understanding of steelhead and coho salmon ocean habitat use lags behind that for other Pacific salmon, presumably due to limited fisheries and lower abundance. There are some data on location from at-sea captures of steelhead, but like studies using CWTs, these are limited by where and when surveys were conducted relative to when fish populations overlapped with the survey area. High resolution chronological data are still lacking in the literature and are necessary to develop a clear understanding of the movements and habitat use of these species, as well as how these movements are influenced by environment and food resources.

In this paper, we investigate the application of archival tags that store temperature data to track the habitat use of juvenile steelhead and coho salmon migrating to sea (smolts), as well as adult steelhead performing second ocean migrations (kelts). We used archival tags to address several objectives. The first objective was to study ocean habitat use and likely migration patterns. Secondly, we sought to characterize freshwater habitat use and thermal environment experienced by juvenile steelhead that delayed or skipped their ocean migration and remained in the river for extended periods of time. Finally, we used thermal profiles from tags that were recovered following predation events to characterize the location of some juvenile salmonid predation and the likely predators. We

conclude with an evaluation of archival tag technologies for addressing the above questions.

Study Site

Scott Creek is a small coastal watershed, approximately 70 km², in central California, 100 km south of San Francisco. Steelhead and coho salmon spawn there naturally, and both populations are subsidized by a small conservation hatchery in the watershed that spawns wild broodstock and releases juveniles at smolt stage (Hayes et al. 2004). Several aspects of the study site make it ideal for archival tagging. The hatchery provided large juvenile fish and served as a tagging laboratory. An adult fish trap and relatively small adult populations (~300 returning adults/species) increased the probability of data logger recovery and enabled the collection of adult steelhead during their return migration to sea for tagging purposes.

Methods

Tag deployment

We began archival tagging in 2003 with one of the smallest archival loggers available. The tag consisted of a temperature logging system, marketed as the I-button (Dallas Semiconductor Corp, subsidiary of Maxim, Sunnyvale California), which collected up to 2,048 data points at 0.5°C resolution (–5–26°C range), with programmable sampling rate. The tag was repackaged in a rubberized coating and distributed for long term marine operation by Alpha mach (Mont-St-Hilaire, QC, Canada) and sold as the "iB-Krill," approximately 25.4 × 13.2 mm and 3.2 g in size. All tags were programmed to maximize sampling duration, by sampling at 4 h intervals, beginning at midnight, sampling six times per day.

Due to concerns about tags interfering with growth and causing drag on juvenile fish, an external attachment method was not considered feasible. Therefore, the tags were surgically implanted into the body cavity of juvenile fish greater than 200 mm fork length and 100 g mass. While it was possible to collect wild steelhead in this size range, wild juvenile coho rarely exceed 140 mm prior to ocean entry. Hatchery fish of both species were used for tagging in place of the smaller wild fish. Hatchery fish were typically scheduled for release between the last week of March and first week of April. Tagging surgeries were typically conducted at least one week before this. In 2003 and 2006, hatchery steelhead had not reached the minimum size threshold, therefore some fish were held back and reared under low density, high food ration conditions, and eventually tagged and released during May or June.

During the surgeries, fish were anesthetized and placed dorsal side down in a V-board lined with moist foam. A 2–3 cm incision was made in the ventral surface approximately 1 cm forward of the pelvic girdle extending towards the head. Tags were presterilized in 80% ethanol, dipped in sterile water and then inserted into the body cavity along with a Passive Integrated Transponder (PIT) tag. The incision was closed with 2–3 surgical staples or polypropylene sutures. The entire procedure typically took 2–3 min and the fish was allowed to recover and observed for at least one week prior to release in the lower section of Scott Creek, approximately 1 km from the ocean.

Adult steelhead kelts received a tag through surgical implantation or external attachment. External attachment used a 2-point attachment similar to the methods of Hinke et al. (2005a, 2005b) and Walker et al. (2000). Briefly, adult female steelhead were captured after spawning during their downstream migration and lightly anesthetized. A pair of 10 cm 12 gauge needles were pushed through

the dorsal musculature approximately 3 cm below the dorsal fin and 2.5 cm apart. Two nickel pins were pushed through attachment holes on the tag, then into the exposed ends of the 12 gauge needles and through the dorsal part of the fish. The needles were then removed, leaving the ends of the nickel pins exposed on the opposite side of the fish. Small plastic washers were placed over the pins and the ends of the pins were clipped to leave about 1 cm of pin exposed. The ends were then rolled down with needle-nose pliers to prevent the washer from slipping off. In 2007 and 2008, 14 tags were also surgically implanted in adults, using similar procedures to those used for the aforementioned juveniles. Surgeries were conducted streamside at the Scott Creek weir trapping station. Kelts were allowed to recover in a flow-through live box placed in the stream and were released once they appeared to be completely recovered and ready for rapid swimming (typically after 20 min). Adult tagging was restricted to females, which typically have higher marine survival rates than males in this system (Hayes unpublished data).

Tag recovery and calibration

Tags were recovered through several methods, including some unexpected ones. The plan was to recover tags from fish on return spawning migrations as they entered the adult fish trap on the lower section of the Scott Creek watershed. Fish carrying external temperature loggers were restrained while a pair of small wire cutters was used to clip the pins holding the tag to the dorsal surface of the fish. The tag and pins were then removed, the fish was measured for length and weight and scale samples were taken, followed by recovery and release. All fish returning through the fish trap were scanned for PIT tags and cross referenced with a list of fish carrying internal data loggers. Fish recovered with internal data loggers were transported to the hatchery,

anesthetized and the tag removed surgically. This required a 3–5 cm incision on the ventral midline, just forward of the pelvic girdle. There was typically little tissue attached to the tag, and it was removed with hemostats, followed by suturing the incision. After a 2–3 d recovery period, fish were released from the hatchery to continue spawning in the wild. All tags were stamped with a contact number, and in several cases tags were returned from unexpected sources, including three that were found in bird roosting and resting areas and one recovered by a fisherman.

Upon recovery, tags were downloaded using the iButton Viewer 32 TMEX software (Dallas Semiconductor). In most cases, tags were run through a temperature calibration in a water bath from 0–25C to account for potential sensor inaccuracy. A regression curve was established and applied to the raw downloaded data, yielding an accuracy and precision estimated to within 0.25°C. In several situations, there was significant clock drift. To compensate for this, the download file records current clock time of the tag and the downloading computer in the same file. While it was possible to correct for this, it was not clear if drift rates were linear. In several situations tags were analyzed for diurnal temperature changes at sea and/or compared with diurnally changing stream temperatures. In these situations, only tags whose clock drift was less than the time between two sampling points (4 h) at recovery were used.

Environmental measurements

Stream water temperatures were measured on an hourly basis at two locations in the watershed, upstream and at the estuary, (Figure 1) initially with IB-Cod temperature loggers (Alpha Mach, Mont St-Hilaire, Quebec, May 2002 to June 2003) switching to Onset Tidbits (Onset Computer Corp. Pocasset, Massachusetts) in the upper watershed site and YSI 600 XLM data loggers (YSI Inc.

Yellow Springs, Ohio) in the estuary (July 2003 through December 2008).

Sea surface temperature (SST) data from the Pacific Ocean north of 25° were obtained from NOAA Coast Watch (http://coastwatch. pfel.noaa.gov/data.html) at a 0.1° resolution. We used the blended sea surface temperature product, which incorporated data from numerous sources: Aqua, NOAA GOES-10, NOAA GOES-12, NOAA POES-17 and POES-18. SST data across the ocean were averaged for each pixel for each month except for during entry and return months during which the fish did not spend the entirety of the month at sea. During these times, the SST temperature data were averaged over the period of the month during which the fish was known to be at sea as determined from the archival temperature data pattern.

Data Analysis

For constructing figures with potential ocean travel range estimates, point to point swim speed times for steelhead were collected from the literature (Burgner et al. 1992; McKinnell et al. 1997; Walker et al. 2000). A total of 77 estimates were found that enabled a calculation of swim speed in km/d. We restricted time between tagging and recapture to events less than 365 d, yielding 57 data points. The maximum estimated speed was 85 km/d and the mean was 24 km/d. For conservative purposes of making maximum range estimates, we used the speed that was two standard deviations above the mean, or 64 km/d.

For ocean temperature records, the point of stream departure or reentry was determined from overlaying temperature data from the estuary on the fish tag data record. The ocean was typically several degrees cooler than the stream in March and April and warmer in February. In addition the stream was subject to daily temperature fluctuations of at least
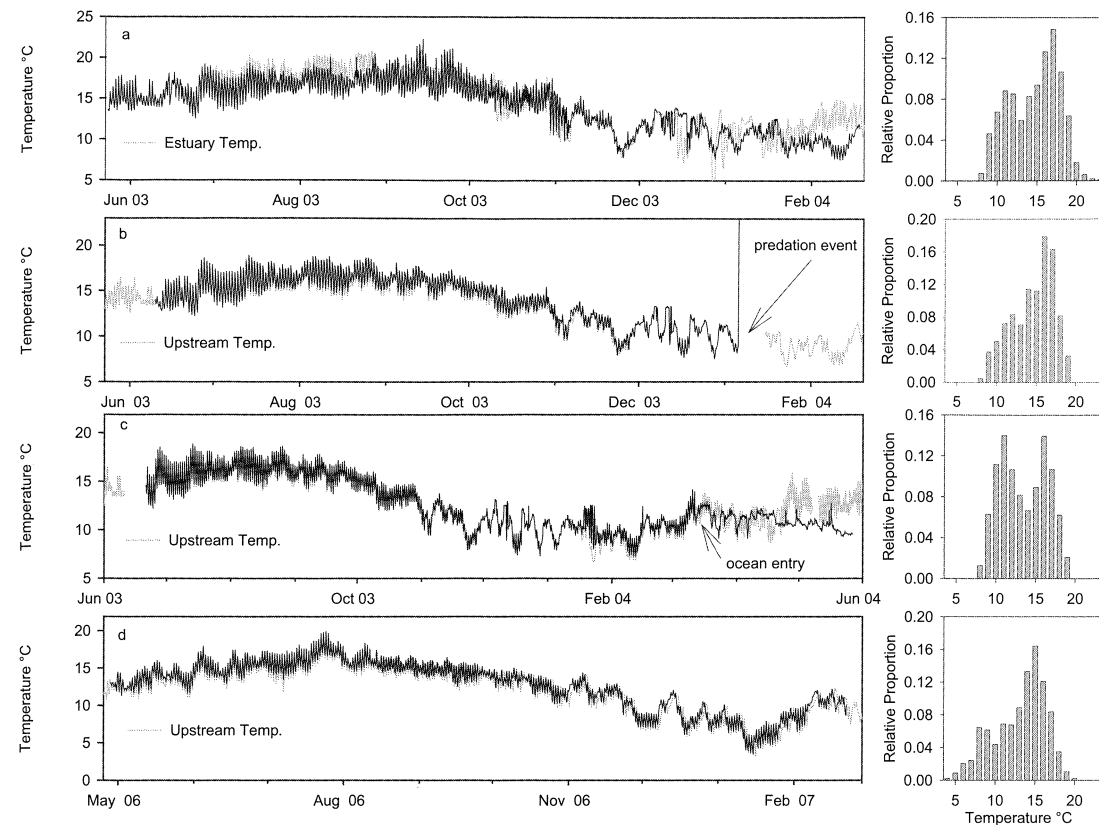
FIGURE 1. Temperature data logger (black line) and corresponding frequency distributions for juvenile steelhead *Oncorhynchus mykiss* that reared in Scott Creek. Estuary or stream temperature data are underlain in gray to demonstrate the relative temperatures of the watershed. Box 1a. shows data for a wild steelhead juvenile from the estuary beginning in May 2003. Box 1b. shows a hatchery steelhead smolt that was released in June 2003 and consumed by a predator in January 2004. Box 1c. shows a hatchery steelhead smolt that was released in June 2003, staying in the stream until March 2004, then entering the ocean, and tag memory filled in late May 2004. Box 1d shows a hatchery steelhead smolt that was tagged in April 2006, resighted several times in the lower watershed throughout the year and tag recovered in February 2007.

two degrees, corresponding to early morning lows and mid afternoon highs that were not present in the ocean portion of fish records. This usually enabled a clear determination of when fish left or re-entered the river to within a 4 h point in time. Stream temperature data were then removed from tag records for which ocean data were available. Extensive evidence from the literature indicates steelhead are very surface oriented, and the vast majority of the data were likely to reflect sea-surface temperatures in the epipelagic zone (Burgner et al. 1992; Nielsen and Zimmer-

man 2008; Welch et al. 1998b). Therefore monthly frequency distributions of temperature were generated for each archival tag record and were presumed to reflect measurements made at the sea surface. Based on the literature (Walker et al. 2004; Walker et al. 2005; Walker et al. 2001; Walker et al. 2000; Welch et al. 1998a), it did not seem reasonable to make similar assumptions for coho salmon.

We used the archival data from recovered steelhead combined with observed SST data to determine probable habitat within the Pa-

cific Ocean, similar to the methods of Hinke et al. (2005a). Temperature data from each recovered steelhead archival tag were binned into 0.25°C bins, and frequency distributions were determined for each month at sea. We then compared the frequency distributions to the Pacific Ocean SST data to determine possible areas of suitable habitat. The Pacific Ocean SST data were averaged for each month and represented on a gray scale from black (−3°C) to white (34°C), with a color spatial resolution of roughly 0.1 degree (~11 km). Sea surface temperatures that corresponded to temperatures recorded by archival tags were color coded on a rainbow scale with dark blue representing a minimum probability of 0.1, and red matching the highest probability location in a given month. Independent frequency distributions were generated for each month relative to SST data. The full color scale was used in each figure to maximize the potential range contrast, and due to variations in peak probability values between months, was not scaled consistently across figures. We then restricted the identified area of available habitat to the most probable areas occupied by the fish by applying a 64 km/d migration rate. From the origin of ocean entry, we applied increasingly large circles representing maximum distance possible from origin until the radius of the circles reached a distance at which the fish would have had to return to arrive back at the origin by the return date. In the end, this analysis included all the data from the Pacific Ocean within the radius of possible migration distances from Scott Creek for each month at sea. By late summer months, nearly the entirety of the ocean was within the possible range of steelhead salmon (~12,000 km radius).

Results

A total of 579 archival tags were deployed on coho salmon (*n* = 260) and steelhead (*n* =

319). Of these, 9 tags were recovered through several methods (Tables 1 and 2). Three tags, one coho and two steelhead, were found deposited on beaches where predators reside and returned to us. One tag was returned to us by a fisherman who captured a coho salmon. Four steelhead were recovered with internal tags requiring surgical removal. Of these, only one had gone to sea, while the other three remained in the stream. One of the three stream fish had apparently expelled the tag, as it could not be found during the surgery and there was a 2 × 3 cm patch of scar tissue on the ventral body wall near where the tag had been implanted. For the hatchery steelhead smolts, where tagging and release were delayed to increase size, an increased residualization rate was observed with many fish choosing not to leave the stream in the year they were released.

Sixty-nine tags were deployed on steelhead female kelts. Two attachment methods were used, with the majority of tags deployed with an external mount during 2004 and 2007. Four tags were implanted in the body cavity in 2007 and an additional 10 tags were implanted in adult kelts in 2008. Of these, two external tags were recovered.

Steelhead juvenile freshwater thermal environment

Four juvenile steelhead tag records (1 wild, 3 hatchery) showed extensive freshwater residency periods (Figure 1). One wild smolt was collected from and released back to the estuary. This fish was recovered 10 months later at the weir. During the surgery, it was apparent that it was female and was sexually mature with eggs ready for spawning. The tag data indicated that the fish had spent much of its time in the estuary (Figure 1a). A direct comparison to estuary temperatures showed the fish spent 59.6% of its time within 1°C of the estuary surface temperature sensor. In addition the fish spent 32.7% of its

TABLE 1. Summary of tag deployments and recoveries by species. Both internal (in) and external (ex) attachments were used with kelts. Some steelhead *Oncorhynchus mykiss* smolt deployments were delayed (d) in some years to increase fish size.

			mean length (mm)	# returned from ocean	# recovered in stream	# recovered elsewhere	# residualized
Coho hatchery smolts							
	2003	30	212	0	0	0	
	2006	214	240	1*	0	2	
	2007	16	258	0	0	0	
Steelhead							
hatchery smolts	2003	28	223	0	0	0	
	2003d	78	246	1	1	1	10
	2006	59	208	0	0	1	
	2006d	49	220	0	1	0	1
wild smolts	2003	4	287	0	1	0	1
	2005	30	219	0	0	0	1
kelts	2004	17 ex	671	1	1	0	
	2007	38 ex, 4 in	665	1	1	0	
	2008	10 in	667	0	0	0	

*not recovered but detected by instream PIT reader reentering river

TABLE 2. Meta data of recovered archival tags.

Species	Age at deployment	Origin	Deployment date	Recovery date	# of days	Fork Length (cm) deployment	Fork Length (cm) recovery	Attachment	Data result
Coho	smolt	hatchery	03/02/06	09/07/06	189	26.9	~45	internal	ocean
Coho	smolt	hatchery	03/14/06	05/31/06	78	21.3		internal	predation
Steelhead	smolt	wild	05/14/03	02/18/04	280	32.7	38.0	internal	stream
Steelhead	smolt	hatchery	06/09/03	02/10/04	246			internal	stream & predation
Steelhead	smolt	hatchery	06/18/03	02/04/05	597	22.3	55.0	internal	stream & ocean
Steelhead	smolt	hatchery	04/25/06	02/23/07	304	22.2	23.5	internal	stream
Steelhead	smolt	hatchery	03/29/06	06/08/06	71	20.3		internal	predation
Steelhead	Kelt	hatchery	04/20/07	02/07/08	293	66.0	72.0	external	ocean
Steelhead	Kelt	wild	03/05/04	02/15/05	347	49.5	56.0	external	ocean

time in water more than 1°C cooler than estuary temperatures, and 7.5% of its time in water more than 1°C warmer than estuary temperatures. During July and August of 2004, the fish was residing in cooler waters, corresponding more to temperatures from a sensor on the bottom of the estuary (data not shown). During September, the fish spent a great deal of time in water that was greater than 20°C, peaking at 23°C, despite having cooler refuge habitat available upstream (Figure 1b). During January, the fish appeared to move into cooler temperatures corresponding to upstream water temperatures (Figure 1b) and was eventually collected at the upstream fish trap on February 18th.

Three additional data loggers were recovered from hatchery steelhead smolts that showed extensive freshwater residence periods (Figure 1b–d). In each case, these were fish that experienced a delayed release. All three fish experienced temperatures that corresponded to upstream temperatures. These temperatures were lower than estuary temperatures during summer and fall months but were similar during the winter/spring high flow season. One fish (Figure 1b) spent seven months in the stream. A comparison to a stream temperature sensor indicated the fish spent 92% of its time in water temperatures within 1°C of the stream sensor and deviated by more than 2°C only once. Another fish (Figure 1c) spent 10 months instream before entering the ocean in March 2004. This assumption was based on the cessation of diurnal temperature fluctuations in the temperature record, which would have been very unlikely in the stream environment. A third fish, tagged in 2006 (Figure 1d), was recaptured three times throughout the year within a 300 m stretch of stream. This fish showed a near perfect correspondence with stream temperature from the sensor in that region. Exact comparisons were not made due to a 25 h drift in the tag clock.

Predation insights

Three loggers were recovered with temperature profiles indicating that fish had been consumed by a warm blooded animal. It is possible these fish died and were eaten by scavengers or were captured by predators. One tag from a steelhead was recovered on Scott Creek beach 7 months after it was deployed (Figure 1b, Figure 2a). The other two tags, one from a steelhead and one from a coho salmon were recovered on Año Nuevo Island, approximately 12 km north of the watershed. An additional seven PIT tags from smolts tagged with temperature loggers were found on the island as well, for a total of 5 coho salmon and 4 steelhead. The upper temperature limit of the archival tag was only 25°C, limiting the ability to measure core temperatures of the predator. In all three cases, the temperatures of the tag corresponded to estuary temperatures for several days leading up to the moment of predation (Figure 2).

Steelhead and coho ocean thermal environment

Archival tags with ocean temperature data were recovered from two steelhead kelts (Figure 3), one steelhead smolt (Figure 1c; March–May 2004) and one coho smolt (Figure 3). An additional tagged coho salmon return was detected by instream PIT tag readers, but the fish evaded recapture. The two steelhead from 2004 experienced temperatures between 7.8 and 14.1°C. The steelhead kelt tagged in 2007 experienced temperature ranges from 7.2 to 14.8°C. Despite differences in age-class, hatchery and wild origin, and years between tag recoveries, the steelhead showed very similar temperature patterns. The coho smolt tagged in 2007 experienced temperature ranges from 9.8 to 17.7°C during 6 months at sea. The coho salmon was recaptured approximately 25 km to the southeast
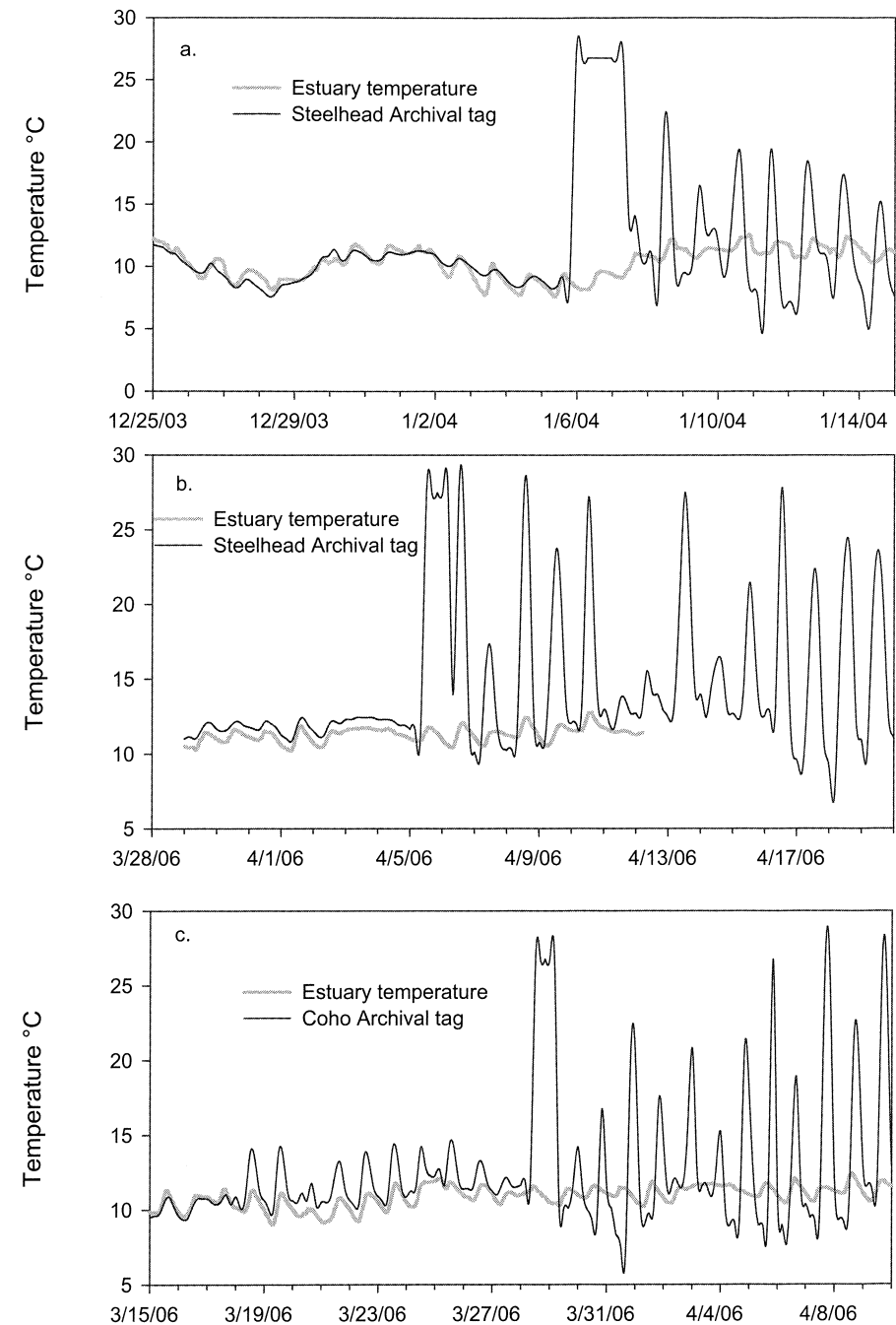

FIGURE 2. Temperature traces of fish consumed by warm blooded predators. Trends show fish tag data overlaid on matching estuary temperature data, followed by predation event, and subsequent deposit of tag onto a terrestrial environment, including (a) a blow up of the hatchery steelhead from Fig 1b with the tag deposited on Scott Creek beach in 2004, (b) a hatchery steelhead and (c) a hatchery coho tagged in March 2006, and tags were recovered on Año Nuevo Island later that summer.
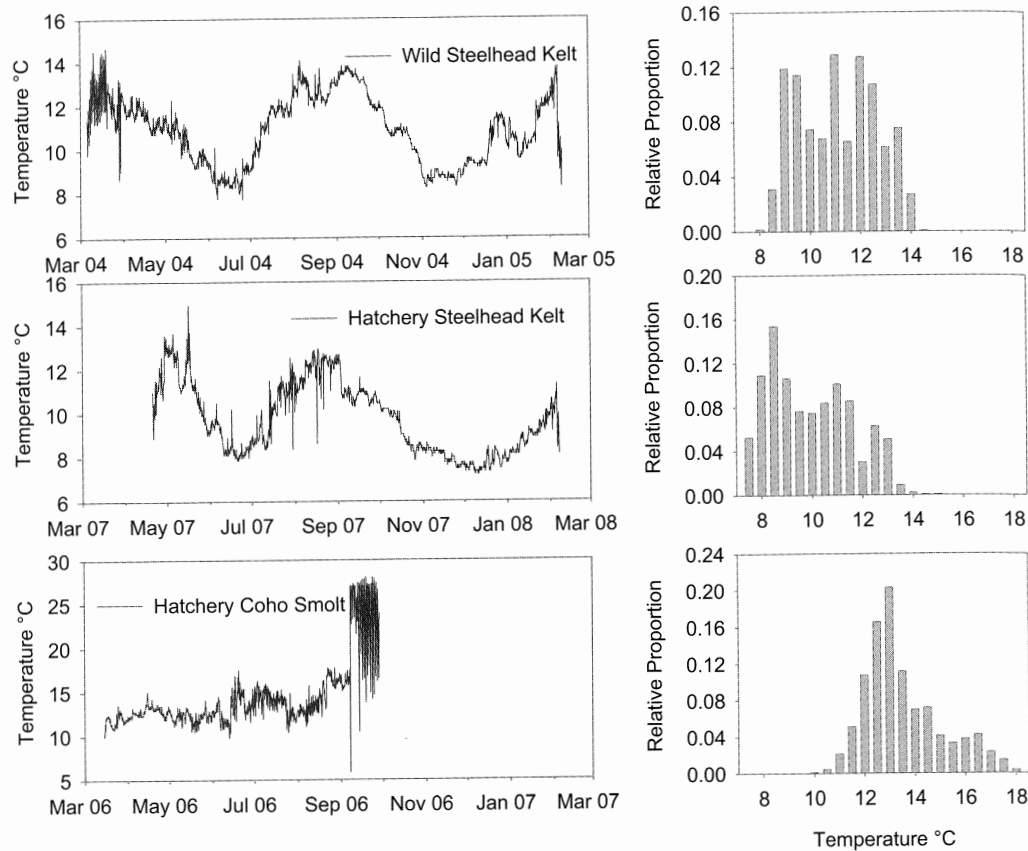
Figure 3. Raw temperature logger data and frequency distributions of two steelhead kelts and one coho smolt that went to sea.

Figure 4. Comparison of monthly mean daily temperatures experienced by the two steelhead kelts for 800 and 1600 during their migration showing the relative lack of diurnal temperature fluctuations in the two records.

of Scott Creek, off of the Santa Cruz Wharf, which was an unexpected location for a coho salmon to be caught in September.

The steelhead data were examined for diurnal changes in temperature, indicative of vertical migration patterns in the water column. The coolest temperatures were typically observed during the 0800 hours reading and the warmest temperatures typically experienced during the 1600 hours reading (Figure 4). There are reports of North American steelhead being found as far west as the Kuril Islands (Myers et al. 2005). If such assumptions were applied to these data, its possible that fish could be in a time zone up to 7 h west of where they were released, which would significantly shift the dawn and dusk

times. While the afternoon record tended to be slightly warmer, there were no differences of biological significance, with many portions of the record showing variations of less than 1°C for weeks at a time, providing little insight into any east-west movement that might otherwise be present if daily vertical migrations occurred.

Working with the assumption that steelhead temperature data were from the surface layer and corresponded to satellite SST data, probable habitat plots were generated based on monthly temperature frequency distributions and potential migration speeds to indicate the likely regions of the ocean where steelhead would be found (Figure 5). For all three steelhead, temperatures at ocean entry
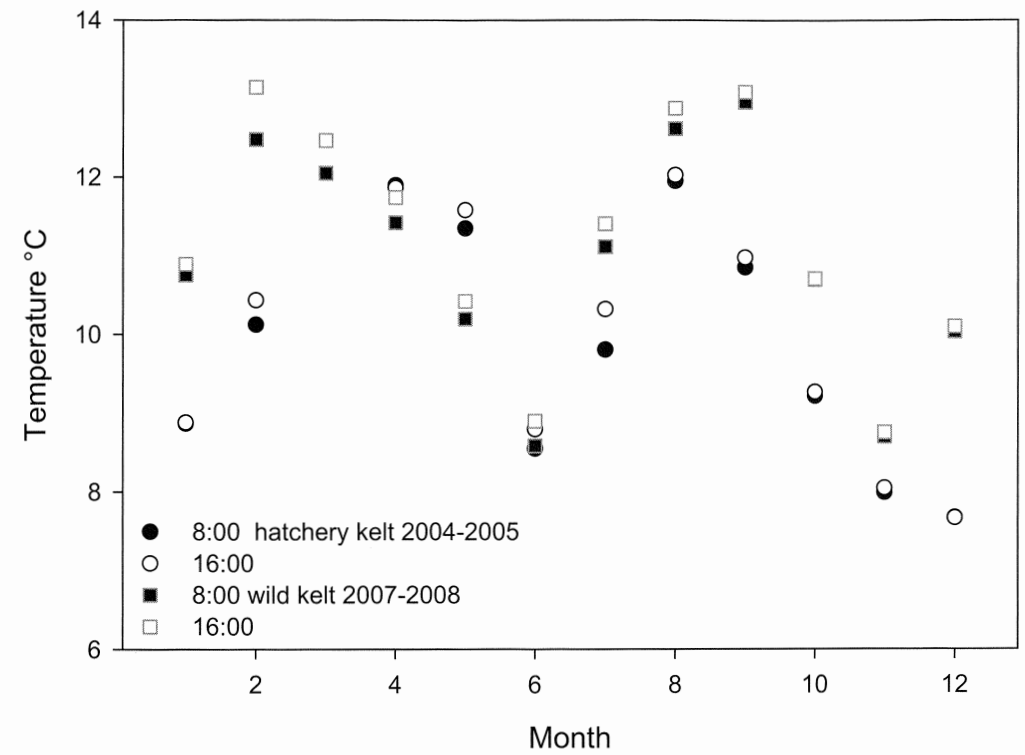
corresponded to temperatures along the central coast. Both 2004 fish entered the ocean in March, while the 2007 fish entered in April. The tracks between the three fish were quite similar, with the 2007 fish initially appearing to lag by approximately one month in geographic location. All three fish experienced temperatures that suggest rapid northwesterly movements, and by the third month to areas corresponding to regions outside the California Current, matching coastal regions between Vancouver Island and Southeast Alaska and extending west into the Gulf of Alaska. Suggested temperature ranges continued pushing north to the Aleutian Islands and west to the coasts of Japan and Russia by September in both 2004 and 2007. Ranges began retracting due to travel-time limitations in October, with southward shifting movements beginning in November. Temperatures

indicated fish were still outside the California Current in December but began corresponding with California temperatures in January and tightly with temperatures in Central California, just prior to stream reentry in February of both years.

Discussion

These data represent some of the first archival tag recoveries for juvenile Pacific salmonids and the first year long records for Pacific salmonids. Despite low tag return rates of less than 1% for smolts and 2% for steelhead kelts, the data acquired provide insights that could not be produced by any other methodology for comparable costs. From just a few tag returns we were able to document the wide freshwater thermal range that juvenile steelhead and, presumably, coho
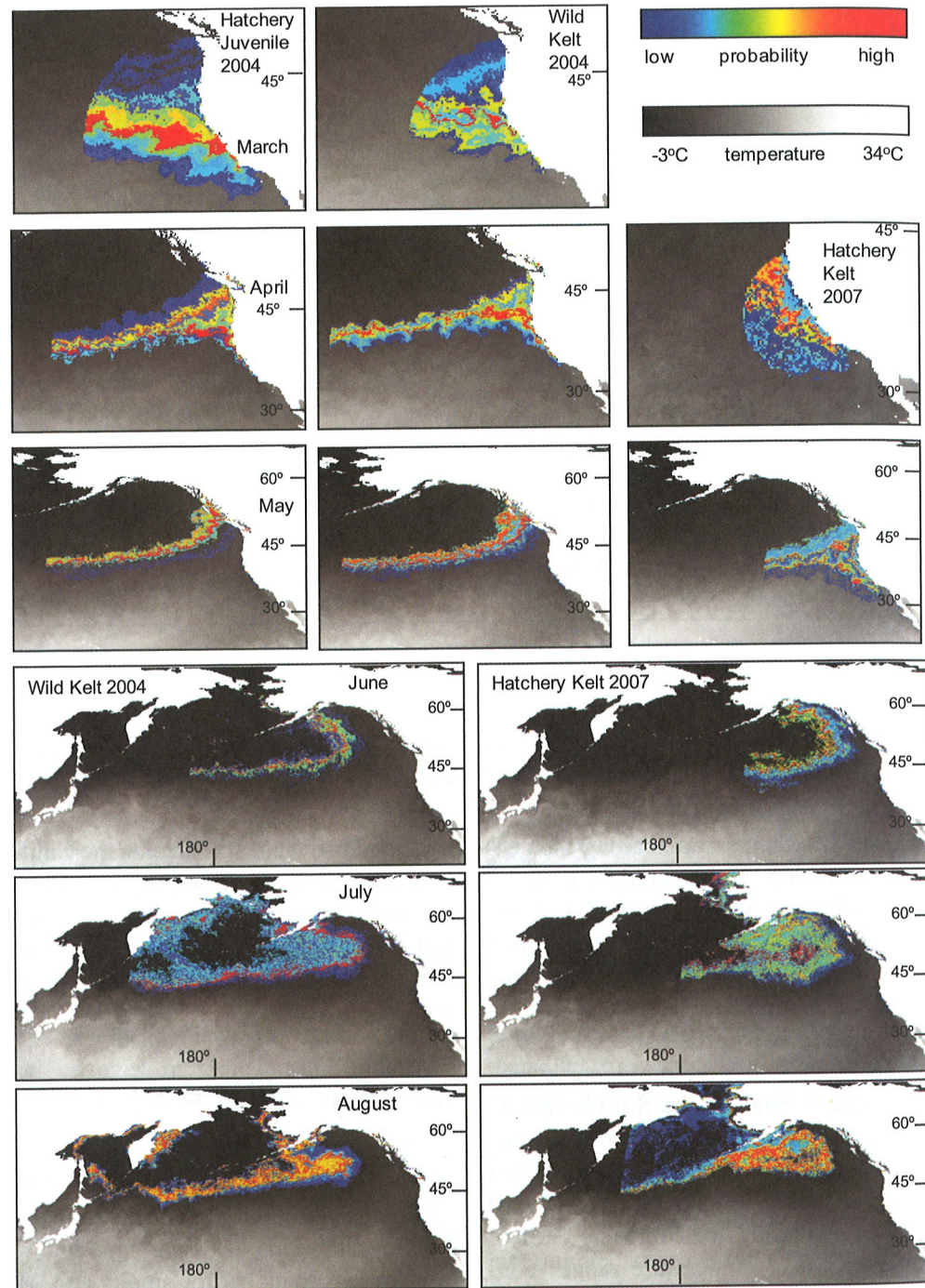
FIGURE 5. Graphical analysis of available steelhead ocean temperature data for one juvenile hatchery steelhead (March–May 2004), one wild female kelt (March 2004–February 2005) and one hatchery female kelt (April 2007–February 2008). The gray scales represent 0.1° (~11 km) SST values averaged for each month. The minimum SST value represented across the figure is –3°C (black) and the maximum value represented is 34°C (white). The color scale represents monthly probability distributions for the SST experienced by the steelhead during each month. The minimum probability value is 0.01 (blue) and the maximum probability value is given in red, with the upper limit varying between months. Pixels without color represent probability values of zero.
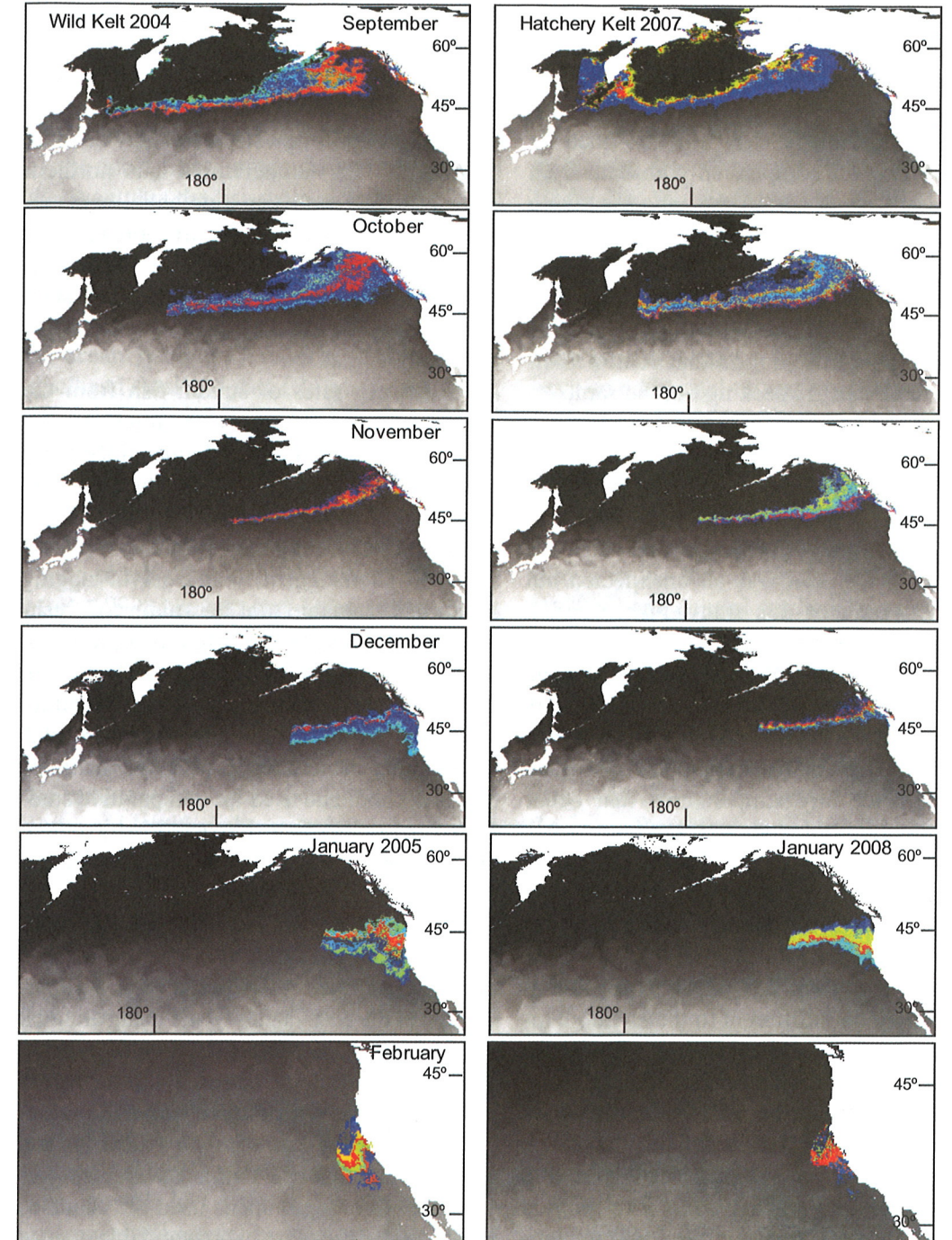
FIGURE 5. Continued.

experience and contrast it with the extreme-ly narrow thermal range of waters maturing steelhead apparently seek out in the marine environment. New data on coho salmon ocean thermal niche were also provided by a tag return, for comparison with data from other researchers across the range studying coho, steelhead and other species. In addition this work shed new light on the habitats in which juvenile steelhead and coho were susceptible to predation. Finally, the data from several tag returns suggest that central California steelhead are seeking out the same regions of the North Pacific as steelhead from other northern populations and are potentially undertaking one of the longest marine migrations known.

Documenting the freshwater thermal habitat of steelhead was an unexpected but valuable result of this study. Fish carrying archival tags in the upstream habitat showed temperatures with high correspondence to the temperatures recorded by temperature loggers in that habitat. While not surprising, it provides evidence that fish are potentially forced to experience any temperatures that occur in shallow coastal streams like Scott Creek, and that there is very little cool refuge habitat should extreme temperatures occur. This implies that juvenile coho salmon are probably experiencing similar thermal environments. Alternatively, steelhead in this population may simply be indifferent to the stream temperature conditions that occurred during the course of this study and didn't bother to seek out thermal refuge habitat. If fish are truly at the mercy of limited variability in stream habitat conditions, it emphasizes the need to maintain healthy riparian canopy to provide thermal cover for potentially more temperature-sensitive species like coho salmon.

In contrast to the upstream habitat, some of the archival data indicated that steelhead also make use of the estuary habitat. This has already been well documented (Bond et al. 2008; Hayes et al. 2008; Hayes et al. 2004),

but it was remarkable to observe that steelhead did not move to accessible cool water habitat even when temperatures were quite warm (>22°C) in the estuary, an indication that central California steelhead may be more tolerant of high temperatures than northern stocks. It also serves as a potential explanation for why coho salmon are not typically observed in the estuary during the warmer summer and fall months in this system (Hayes et al. 2004); they may be restricted to upstream habitat.

Recovery rates of stream fish from the freshwater environment were high. An actual percentage is hard to define, since these recoveries were purely opportunistic and it's likely very high rates could be achieved with concerted collection efforts in shallow streams. This suggests that archival tagging could be a valuable tool for studies of freshwater habitat use. When used in conjunction with instream PIT tag readers (Bond et al. 2007) and high-resolution stream temperature mapping, one could gain tremendous insights into habitat preferences and movements for fish. This could be used for comparative studies of natural habitat, impacted habitats and for evaluating the effectiveness of restoration efforts.

The recovery of archival tags that were consumed by predators was unexpected and serves as a reminder that predators are a component of the ecosystem. While using archival tags to study predation behavior is probably not an ideal strategy, the archival tag recoveries coincided with the recovery of a larger number of PIT tags on Año Nuevo Island (Hayes, unpublished data). Several species of sea birds and pinnipeds used the island as roosting and breeding habitat and this opened up speculation as to which predator was responsible. A higher thermal limit on the tag to measure predator core temperature would have been useful. In either case, all three archival tag recoveries showed tight correspondence to estuary temperatures right up until

the moment of predation, suggesting the fish was captured before entering the ocean. Only one species, the Western Gull *Larus occidentalis*, is found on both the island and in the Scott Creek beach/estuary, which identifies it as the most likely predator, or scavenger in the event that the fish were already dead.

The application of the archival tag temperature data to remotely sensed sea surface temperature data indicates that steelhead from central California use the same region of ocean habitat as reported for all other steelhead stocks to date (Burgner et al. 1992; Myers et al. 2005; Myers et al. 1996; Welch et al. 1998b). The method served to produce surprisingly restricted regions of likely distribution. It did make the assumption that all data were from the surface. But this is well supported by both the literature (Burgner et al. 1992; Nielsen and Zimmerman 2008; Welch et al. 1998b) and limited daily variability in temperature profiles; the fish did not migrate below a thermocline. If some of the data were from depths with cooler temperatures, this would serve to only tighten the temperature distributions and reduce the regions identified by our habitat analysis (Figure 5). The alternative explanation that steelhead are staying at cooler depths in local waters is unlikely. Aside from what would likely be major changes in diet associated with different habitat, adult, and maturing age classes of steelhead are rarely captured in the Chinook salmon fisheries along the California coast, and only a few juvenile steelhead (typically <30 cm) have been captured during 10 years of central California juvenile Chinook salmon research surveys (MacFarlane, unpublished data), but are captured with increasing frequency by surveys off Oregon and Washington (Miller 2006; NWFSC et al. 2009).

While not surprising, it is intriguing that steelhead, which are reported to have the most diverse array of freshwater life history strategies (Satterthwaite et al. 2009; Shapovalov

and Taft 1954), have the most conserved marine life history strategy of all Pacific salmonids. Steelhead from streams from Alaska to northern California have been recovered in similar regions off the Washington and Canadian coast, extending across the gulf of Alaska all the way to Asia (Myers et al. 2005; Myers et al. 1996). The ocean regions we identified for steelhead from central California suggest they may have the longest migration of any Pacific salmon. Compared to fish originating from Oregon streams, fish from Scott Creek have an additional migration distance of 650 km just to reach the latitude of the California border. Even at an upper swim speed of 64 km/d, this would add an additional 21 d to their migration compared to northern California and Oregon populations. This may contribute to the low marine survival (Bond et al. 2008) and coastal gradient of smaller size fish returning to lower latitude rivers (Withler 1966). It is possible that central California steelhead are more limited in the westward extent of their migration, but insufficient data were collected in this study to examine this idea. Addressing this question would require the use of archival tags with light sensors to perform geolocation analysis, although this might be of limited value during winter months (Teo et al. 2004). Alternatively, it may require increased tagging and recapture efforts or genetic stock identification of fish caught at sea.

Of the three California salmon species, Chinook and coho salmon have migration patterns that are coastal and distributed only limited distances relative to the source of their native river mouth (Weitkamp 2010; Weitkamp 2012, this volume; Weitkamp and Neely 2002). Within the California Current, the population dynamics of both species appear to be tied to local, physical, and biological oceanographic processes (Botsford and Lawrence 2002; Wells et al. 2008b; Wells et al. 2008c; Wells et al. 2007). However, it is likely that California steelhead populations

are relatively independent of local conditions, and their populations may track better with oceanographic variables that influence survival of more pelagic Alaskan salmon populations.

It has been suggested that both steelhead and sockeye salmon have energetic optima that restrict their growth potential to certain thermal windows in the marine environment (Welch et al. 1998a; Welch et al. 1998b). In contrast, steelhead from the Scott Creek population have been shown to grow rapidly in an estuarine environment (Hayes et al. 2008), and the present study has shown that the estuarine environment includes temperatures well above the marine thermal window. Yet, these estuarine growth rates are less than the marine growth rates observed for Scott Creek steelhead (Hayes, unpublished data), suggesting estuarine growth potential could be limited by the elevated metabolic rates associated with the warm estuary temperatures.

Steelhead restrict themselves to a narrower but warmer band than sockeye (Welch et al. 1998a) and a cooler band than Chinook (Hinke et al. 2005b) or coho salmon (this study, Walker et al. 2001). It may be that steelhead attempt to reduce potential competition with other salmonids by using habitats that other salmon do not, which is their suggested strategy in freshwater (Atcheson 2010; Cederholm et al. 1997; Fraser 1969; Harvey and Nakamoto 1996). Steelhead marine diet may also be tied to a prey item that is dependant upon a specific temperature band, or they are utilizing a niche that involves going offshore to eat fish, squid and plankton rather than compete with juvenile Pacific salmon species for more nearshore resources (Burgner et al. 1992; Miller 2006).

It is interesting to note the timing of steelhead entry and exit from the river was tied to the time of year when the temperatures in their narrow thermal window had shifted far enough south to be present in central California. It may also be that ocean entry and migration is timed to a period before the California Current has begun its accelerated movement south during the spring upwelling season. Welch et al. (1998b) discussed potential impacts of climate change causing ocean warming. In addition to shifting populations north, changing climatic conditions may result in localized warming of ocean water near river mouths and changes in current patterns. If steelhead are physiologically restricted to a narrow range of ocean temperatures, this warming may prevent or alter the timing of their seaward or return migrations.

Several lessons were learned from this study that would enhance future efforts. The first was that delaying the migration of steelhead in order to give them additional growth opportunity tended to increase their potential to residualize (not leave the stream). While this may be a useful tool for some questions, if one's goal is to characterize the marine portion of a life history, delaying migrations should be avoided. During a concurrent study, a group of hatchery steelhead were raised in lower densities in a separate tank at the hatchery facility. At release, those fish were larger and showed little evidence of fin deterioration commonly associated with steelhead reared in higher densities. As expected, these fish experienced a marine survival rate (3.4%) that was much greater than that of their siblings reared at higher densities (0.05%, Hayes, unpublished data), providing a better rearing method for future tagging studies. In addition, providing fish with several weeks to recover following tagging probably increases their chances of marine survival and allows for extra time to observe potential tag rejection. However fish should be tagged early enough to allow time for release during the normal migration window.

In this study, most of the coho salmon were tagged and released in the spring of 2006, unfortunately coinciding with an un-

expected California-wide drop in marine survival associated with fluctuating oceanographic conditions (Lindley et al. 2009; MacFarlane et al. 2008; Wells et al. 2008a). While unforeseeable at the time, it suggests one should plan tagging efforts to distribute tags across several years to buffer against such fluctuations.

Unfortunately, even under the best conditions, marine survival and consequent tag returns of marine fish are low. These studies require large tag budgets to deploy enough tags to ensure some level of success. At this point, archival tag technology is not limiting research on salmonids; rather the issue is more one of cost. Most tag companies have been driven by a research market working on commercial stocks of larger fish or marine mammals where tag recovery rates are higher. In addition, many tag technologies were prototype-tested on pinnipeds over the past two decades due to the high return rates (Boehlert et al. 2001; Boehlert et al. 2002; Costa 1993). As tag technology has evolved, manufacturers have phased out older technologies to keep up with the marine mammal and large-fish market demand for new tags with more memory and new sensors. This has weakened the supply of small, simple and economical tags. In addition, it is difficult to convince funding sources to finance the tagging of fish with an expected return rate of 5% or less. These agencies, often willing to fund $100,000 for 10 marine mammal tags with an expected return of 10 tags, need to be persuaded that there is equal merit in deploying 500 fish tags for the same budget to get 10 returns. While the tag return rates in this study were low, the data yield for a tag budget of approximately $25,000 far outweighed the cost of any off-shore ship-based net survey, and nonship based acoustic receiver arrays are only in early developmental stages and limited in their availability to track fish in habitats off continental shelf breaks.

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