

Observations of Steelhead in the California Current Lead to a Marine-Based Hypothesis for the “Half-Pounder” Life History, with Climate Change Implications for Anadromy

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Hayes, S.A., A.J. Ammann, J.A. Harding, J.L. Hassrick, L. deWitt, and C.A. Morgan. 2016. Observations of steelhead in the California Current lead to a marine-based hypothesis for the “half-pounder” life history, with climate change implications for anadromy. *N. Pac. Anadr. Fish Comm. Bull.* 6: 97–105. doi:10.23849/npafcb6/97.105.

Abstract: Steelhead typically spend little time in the California Current. Most emigrate each spring to the North Pacific for one or more years. During this migration, they track a narrow range of sea surface temperatures (SST). However, ship surveys off Oregon and northern California during 2007 and 2010–2014 observed steelhead in late June through August in the Klamath region where a microclimate corresponding to steelhead preferred SST persists through summer before warming in September. Cooler SST in the Klamath region may explain the presence of a life history, known as a “half-pounder”. Spring smolts remaining in this cool coastal region for the summer are eventually cut off from migratory pathways with preferred SST. We hypothesize that fish choose to retreat into local rivers to avoid a warming ocean in autumn. While the half-pounder life history is only common in a couple of regions, it has implications for all steelhead life histories at larger spatial scales. Specifically the 2014–2015 “warm blob” may have blocked thermal migratory corridors during winter and spring migrations for southern stocks. Expanded warming periods could lead to disruptions in the space-time continuum of these marine pathways with respect to acceptable SSTs, restricting access to ocean ecosystems for fish with anadromous life histories. An outstanding question for California steelhead is whether migration pathways will remain stable, or whether connectivity to North Pacific waters will change under potential climate change scenarios.

Keywords: Steelhead, half-pounder, climate change, marine life history, sea surface temperature

INTRODUCTION

Strong association with narrow water temperature ranges in the marine environment is a characteristic of many Pacific salmon species (Welch et al. 1998a, b; Hinke et al. 2005; Abdul-Aziz et al. 2011) and is a key indicator of available habitat, especially for epipelagic species. Aided by this knowledge and satellite-derived sea surface temperature (SST) data, researchers can estimate probable oceanic distributions of several salmon species based on archival temperature logger recoveries without other geo-referenced tools (Friedland et al. 2001, 2003; Hinke et al. 2005; Hayes et al. 2012). Of these species, data from electronic tags and diet indicate that steelhead (*Oncorhynchus mykiss*) are the most surface-oriented salmonid, spending more than 95%

of their time there. This marine habitat use pattern is nearly two dimensional and tightly linked to SST (Walker et al. 2007; Nielson et al. 2011; Atcheson et al. 2012).

Welch et al. (1998b) reported steelhead caught on the North Pacific high seas spend the majority of their time in the 8–14°C temperature range. Similar results have been observed for steelhead migrating from California rivers into the California Current, an eastern boundary current that moves southward along the western coast of North America from British Columbia to southern Baja California (Teo et al. 2011; Hayes et al. 2012). For most stocks emigrating from North American rivers that drain into the California Current these temperatures are typically available during the winter and spring seasons but ultimately fish are thought to move north into the Gulf of Alaska and beyond as coastal

Table 1. Number of individuals captured and fork length data for steelhead caught in SWFSC surveys between 2007 and 2014. * 2007 fish were measured after being frozen, which typically results in ~5% decrease in length. The percentage of adipose-fin clipped steelhead indicates the percentage of hatchery-produced fish in the catch.

Year	Total caught (n)	Mean fork length (cm)	SD	Min	Max	% adipose-fin clipped	Survey dates
2007	21	27.6*	1.3	25.2	30	14	August
2010	1	32.5				100	June/July
2011	66	27.1	6.3	19.1	53.2	21	June/July
	1	32.0				0	September
2012	37	23.5	3.5	17.2	31	14	June/July
2013	56	30.2	4.8	22.5	54	39	July
	0						September
2014	10	36.4	11.9	23.4	56.8	30	July

temperatures warm during summer months. This theory of northward movement is supported by ocean surface trawl and purse seine sampling that found steelhead during May and June in coastal waters off Oregon and Washington but not during subsequent efforts in the later summer months (Percy et al. 1990; Daly et al. 2014). Further south off central California, only three to four steelhead were observed over ten years of summer trawl surveys in the Gulf of Farallones (Hayes and Kocik 2014).

However, in August of 2007, the National Marine Fisheries Service Southwest Fisheries Science Center (NMFS-SWFSC) conducted an exploratory trawl survey from central California to southern Oregon and encountered 21 steelhead in northern California. Based on these observations, we aimed to determine the prevalence and abundance of fish off California and southern Oregon across multiple years (including both summer and fall) to determine coastal residency, and compare the distributions of SST to determine if it influenced the extent of coastal distribution. We also investigated the timing, size class, and specific region(s) where steelhead were observed in the 2007 survey. In particular, we looked for characteristics consistent with a life-history phenotype from that region known as a "half-pounder". The half-pounder life history is characterized by ocean entry as a spring smolt, several months rearing at sea, and a return to the river in early fall as a non-reproductively mature fish ranging from 20–40 cm in length and weighing approximately a half pound (fish of this length tend to range from 200–500 g). While fairly rare throughout the steelhead range, this life history is quite common in the Klamath region, the area bounded by the Klamath, Eel, and Rogue rivers of northern California and southern Oregon (Snyder 1925; Kesner and Barnhart 1972; Lee 2015). The half-pounder life history is also observed in western streams of the Kamchatka Peninsula in Russia, where they are reported to return in the fall and overwinter, particularly in the Utkolok River on the west coast of the peninsula. (McPhee et al. 2007; Pavlov and Savvaitova 2008). The benefit of this

abbreviated ocean migration and premature return to rivers remains a topic of debate as there are no clear survival or growth advantages and many "half-pounders" ultimately go to sea again the following year to complete a normal steelhead ocean rearing cycle (Busby et al. 1996).

The observation of juvenile and immature steelhead in marine waters off northern California led to a mechanistic hypothesis for the existence of the half-pounder life history strategy. We speculated that this life history could result if marine microclimates conforming to steelhead preferred SSTs persisted into summer months while surrounding marine regions warmed beyond steelhead tolerance, effectively creating a trap. If this microclimate breaks down (warms) in the fall, steelhead in such a region would be left with one of four options: (1) persist or migrate through waters above their preferred marine temperature range, (2) descend to cooler, deeper waters, (3) return to one of the rivers in the region to overwinter in fresh water, or (4) perish. There is little published evidence that steelhead exhibit either of the first two behavioral options.

Here, we first investigate the potential seasonal distribution of juvenile steelhead in coastal waters off south-

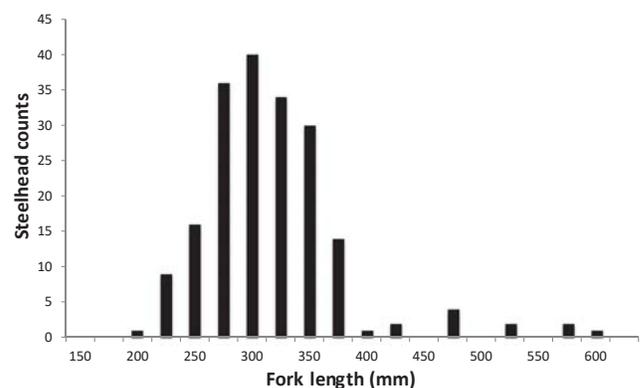


Fig. 1. Size-frequency distributions of steelhead caught in SWFSC survey between 2007 and 2014.

ern Oregon and northern California to ask the question: are juvenile steelhead commonly observed in coastal waters in this region, and are they associated with specific habitat features? Second, we investigate whether marine habitat dynamics supporting our mechanistic hypothesis exist in regions where the half-pounder life history occurs both in northern California-southern Oregon and the Kamchatka peninsula in Russia. Together, these investigations are used to discuss how steelhead stocks may respond under potential climate change scenarios that include a significant increase in SST across sections of the California Current.

MATERIALS AND METHODS

Since 2010, the NMFS-SWFSC has conducted a standardized annual summer salmon survey between mid-June and mid-July, and biannually in September, covering the

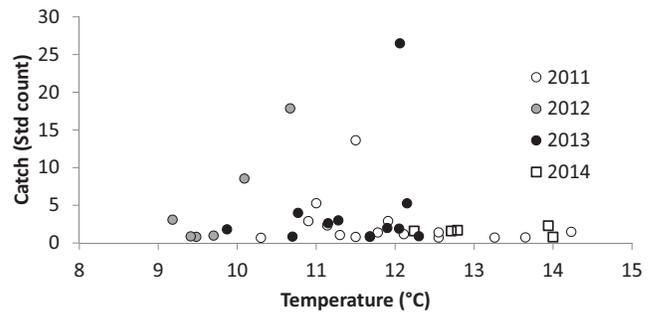


Fig. 2. Sea surface temperature measured by the shipboard thermosalinometer at the sampling station at the mid-point of the trawl line on which steelhead were caught. Std. count is a catch per unit effort metric with total count of steelhead caught in one trawl standardized to 1 million cubic meters of water—the approximate volume of one 30-min trawl.

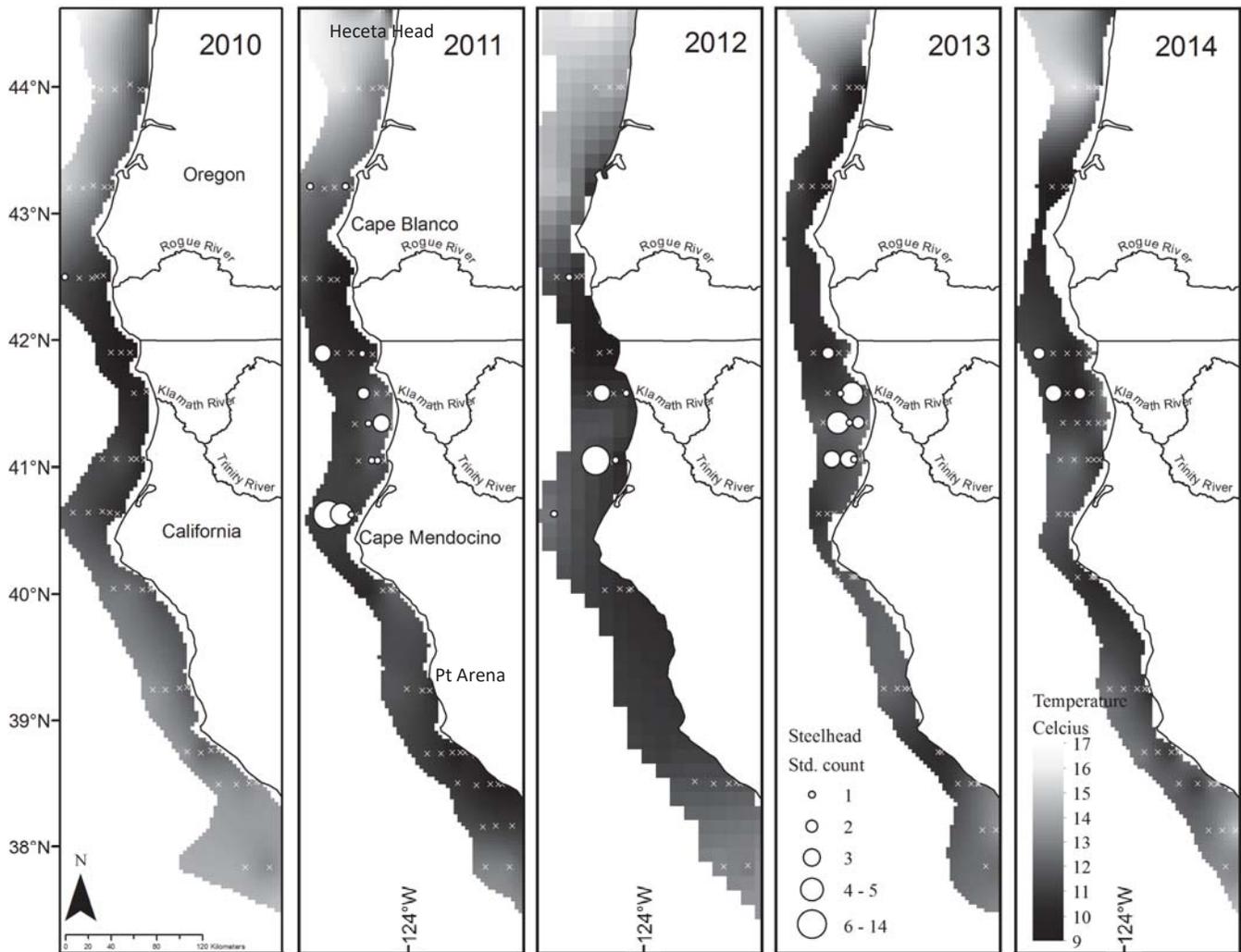


Fig. 3. Steelhead captures from ocean trawl surveys from 2010 to 2014 are denoted by white circles. Temperature data based on real-time SST data collected by shipboard thermosalinometer were interpolated by kriging.

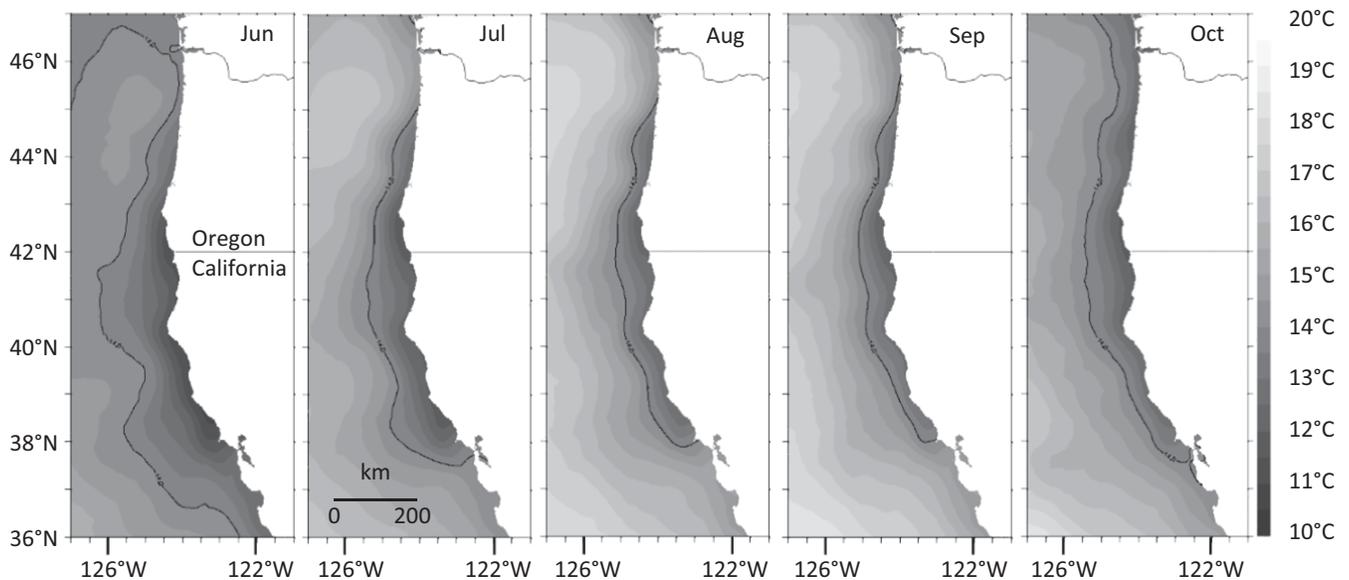


Fig. 4. Monthly mean MUR SST data from June to October, 2002–2014, for the coastal waters of California and Oregon.

same set of transects and stations. The study area is a narrow strip of coastal ocean between Heceta Head, Oregon (44°00'N) and Pigeon Point, California (37°10'N), a distance of 754 km north to south. The sampling grid consisted of 16 east-west transect lines spaced an average of 50 km apart, although line spacing was not chosen to be uniform. Instead, locations of transects were selected for their general proximity to coastal geographic features that could potentially influence salmon distribution (e.g., rivers) or affect coastal currents (e.g., headlands and bays). Five fixed stations were located on each transect. Stations were chosen using criteria for water depth targets and station spacing, or some compromise between the two. The typical water depth for station 1 (closest to shore) to station 5 (farthest from shore) was 33, 57, 124, 215, and 438 m. Thus, the shelf break usually occurred somewhere between stations 4 and 5, or between stations 3 and 4 in a few locations with a narrow shelf or where a transect crossed a submarine canyon. The typical distance from shore (due west) for stations 1–5 was 4, 8, 15, 25, and 35 km, respectively. Prior to 2010, SWFSC conducted a similar coastal salmon survey with a more restricted sampling area off central California between Point Arena (38°57'N) and Pillar Point (37°30'N) annually from 2000–2005 (Harding et al. 2011) and a more extended survey in 2007.

To collect salmon and associated fish and invertebrates, we used a 264 Nordic Rope Trawl (264 NRT; NET Systems, Bainbridge Island, WA) with 3-m² foam-filled pelagic doors, with each door fitted with 200-lb weight shoes. Net dimensions while fishing were approximately 22-m wide x 18-m high at the mouth and 200-m total length with a 15-mm stretched mesh codend liner. The net was rigged with 70-m bridles and fished with 140 m of warp out. Six large floats (Polyform A5) attached to the net (two on the head-

rope kite and two on each upper wingtip) kept the headrope within 0.5 m of the surface continuously during tows (prior to 2011, smaller Polyform A4 floats were used). Footrope depth was 16–20 m (average 18.2 m) during tows, and a few meters deeper (average 32 m) during layout and haulback. Depth recorders (Reefnet Sensus Ultra dive data recorders, Mississauga, ON, Canada) attached to the headrope and footrope verified deployment depths and measured vertical net spread and temperature. A mechanical flowmeter (General Oceanics, Miami, FL) was towed alongside the boat for the duration of each tow to measure speed and total distance traveled through water. Sets were 30 minutes in duration, except where jellyfish were very abundant, in which case tow time was reduced according to jellyfish density. Tow speed (determined by flowmeter) ranged from 3.0–3.8 kn through water (average 3.5 kn speed through water), and tow distance averaged 3.2 km for completed 30 minute tows. To account for differences in tow distance and duration, fish abundance was standardized to a volume of 106 m³ for all hauls—a standard that is about equal to a tow of 30 minutes at 3.0 kn. Wind and seas permitting, the tow path roughly followed the depth contour and intersected the station coordinates near the midpoint of the tow. Thus, tows usually ran parallel to shore, toward the south or southeast with the prevailing seas and swell.

For each tow, all salmonids were identified and measured for fork length (FL). All juvenile salmonids (80–250 mm FL) were lethally sampled; these were individually frozen in plastic bags for transport back to shore. Immature salmonids (> 250 mm FL) were either kept or released, depending on their condition after capture. Immature salmonids that were lethally sampled were either kept intact and frozen or partially dissected in-situ for transport back to shore and subsequent analysis at the SWFSC laboratory.

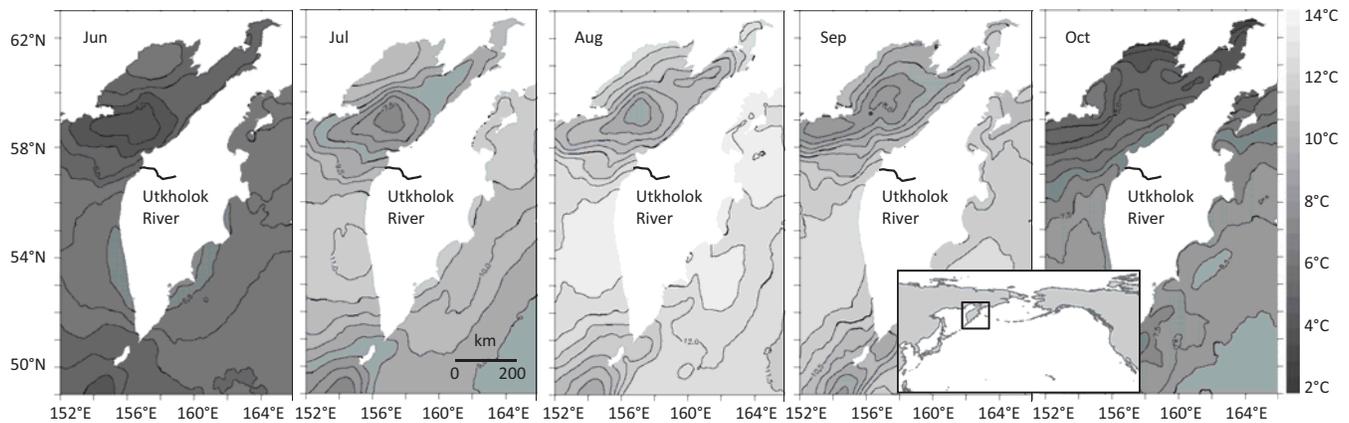


Fig. 5. Monthly mean MUR SST data from June to October, 2002–2014, for the coastal waters of the Kamchatka Peninsula of Russia.

Underway sampling of water temperature was done by continuously pumping seawater through the ship's intake located near the bottom of the hull at around 3 m depth using a Sea-Bird thermosalinometer (TSG Sea-Bird Electronics, Bellevue, WA) or a self-contained underwater fluorescence apparatus (SCUFA, Turner Designs, Sunnyvale, CA). The values were merged with date, time, and position (every 10 s) into a continuous data file representing the entire cruise. Temperature data from the ship-board instruments were spatially interpolated for each survey year using geostatistical methods, generally described as kriging (Johnston et al. 2001). This approach estimates the global trend of a variable across a study area with local dependence in the variance using spatial weight matrices derived from the relative spatial arrangement of surrounding measured values. These spatial weights were constructed from an empirical semivariogram that models the spatial structure of the data. Continuous temperature data were subsampled to every 10th observation and interpolated with ordinary kriging, which allows the mean to vary spatially (i.e. the mean is modeled as constant within each prediction neighborhood).

Satellite-based SST maps were generated in order to compare water temperatures at survey locations to the broader region to understand potential steelhead habitat availability. In order to investigate the mechanistic hypothesis that half-pounder life history is supported by certain marine microclimate patterns, SST maps were also generated for the Kamchatka region in Russia where this life history is also observed. All satellite-based SST maps were generated using Multi-scale Ultra-high Resolution (MUR) Sea Surface Temperature analysis. The MUR data set spans from June 2002 to present, and provides daily global SST at 0.01-degree coordinates at 1-km intervals (http://podaac.jpl.nasa.gov/Multi-scale_Ultra-high_Resolution_MUR-SST and <http://mur.jpl.nasa.gov/InformationText.php>). Data were accessed and downloaded from ERDDAP at: <http://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST.graph>.

RESULTS

Steelhead catches ($n = 192$) from surveys between 2007 and 2014 are summarized in Table 1. Sizes ranged from 175 to 568 mm, 95% of which were under 400 mm, with a peak mode at 275 mm (Fig. 1). Prior to 2001, only a few steelhead were collected during 10 years of ocean surveys primarily focused in Central California. In contrast to catches of Chinook (*O. tshawytscha*) and coho salmon (*O. kisutch*) which are primarily observed on our inshore stations 1 and 2, 87% of steelhead catches occurred on stations 3, 4, and 5 suggesting a more offshore distribution. The increased catch rate in the surveys is thought to be a function of expanded survey range through southern Oregon and gear changes to the trawl net that brought it slightly closer to the surface (Hayes and Kocik 2014). This is anecdotally supported by observations of steelhead being caught during rough seas where the headrope of the trawl regularly comes out of the water between the crest and trough of large wind waves. Due to changes in gear type over the survey years, including increased size of floats in summer 2011 and the addition of marine mammal excluder technology in fall 2011 which allows for some fish to escape the cod-end, no effort was made to provide statistical comparison of results in terms of catch per unit effort. In 2015 the survey was modified to focus on inshore species (Chinook and coho salmon), offshore stations were dropped and very few steelhead were collected.

The majority of steelhead were caught between Cape Blanco, Oregon (42°50'N), and Cape Mendocino, California (42°26'N), with two additional fish caught in 2011 slightly north of Cape Blanco, but south of Coos-Bay Oregon (43°26'N). Sea surface temperatures in all regions where steelhead were collected were < 14.3°C (Figs. 2, 3). In most years of the survey, surface temperatures in the boundary areas to the north, west, and south were already above 14°C in July (Figs. 3, 4). Based upon a longer time series from 2002–2014, the cool microclimate, presumably from coastal upwelling and headland circulation patterns, typically disap-

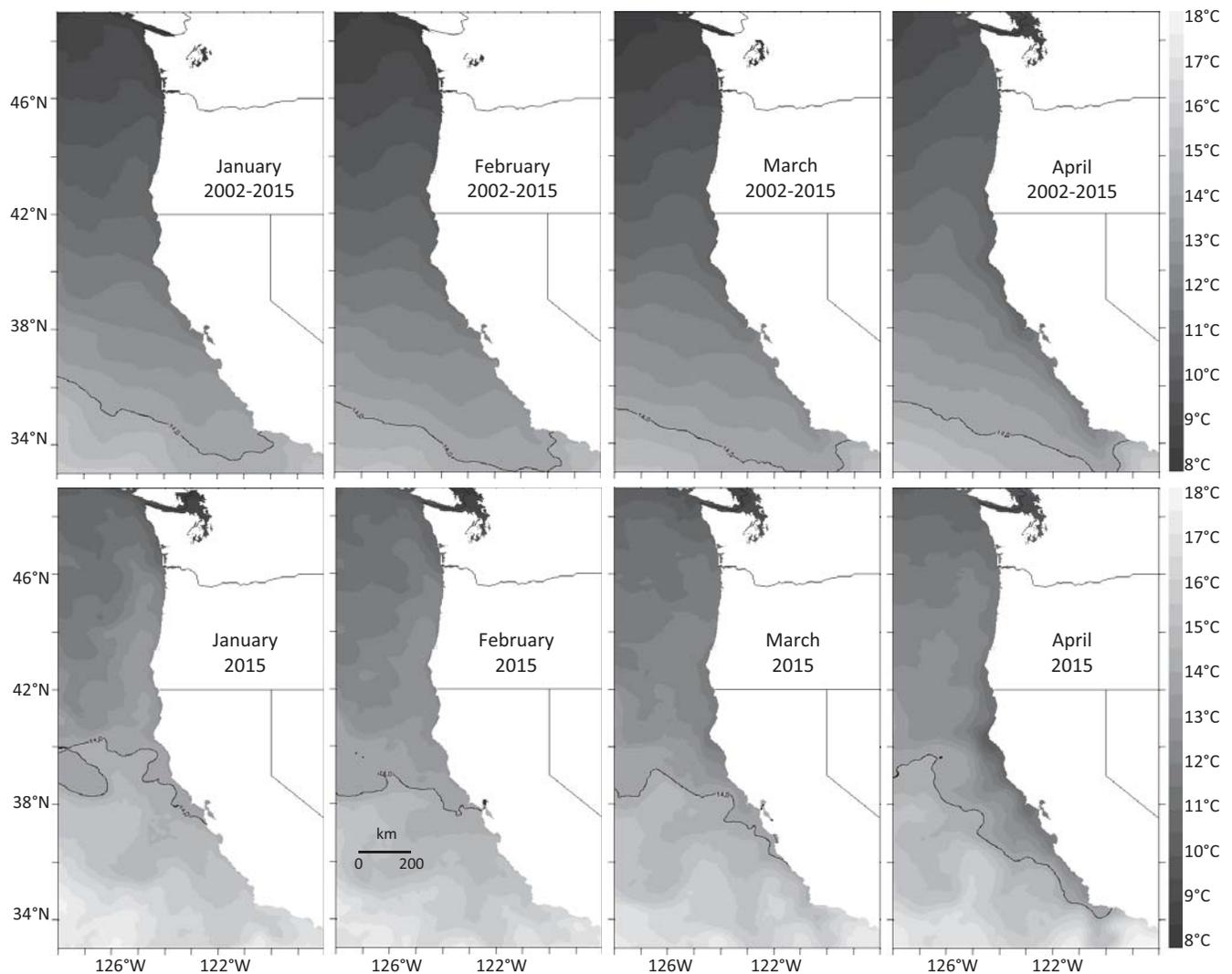


Fig. 6. Schematics of monthly blended MUR SST for the four months (January, February, March, and April) that adult steelhead typically return to and many smolts depart from the California Current. Upper panels show average monthly temperatures for 2002 through 2015. Lower panels show contrasting warm water present during the same months in 2015.

pears around the Oregon and California border (where the Rogue, Klamath, and Trinity rivers enter; see Fig. 3) by September and in many years even that area warms above 14°C for brief periods (Fig. 4).

Plots of the MUR SST data from the Sea of Okhotsk and western Pacific averaged by month across the 13+ year time series reveals a persistent cool water refuge to the north that is regularly isolated from the rest of the western Pacific, with significant warming (12.5°C) peaking in August (Fig 5).

In typical years temperatures as far south as Point Conception in southern California remain well below the steelhead upper observed temperature preference of 14°C . However, as part of a warm temperature anomaly that began in 2014 (Bond et al. 2014), the temperature threshold moved more than 400 km north to a point fluctuating between San Francisco Bay and Monterey Bay during winter and spring of 2015. Plots of the MUR SST data are presented from

the California Current for winter and spring for both typical temperatures steelhead experienced during the return migration in January and February, and their spring smolt migration in March and April over the course of the time series (2002–2015, Fig. 6, top panels) and just in 2015 (Fig. 6, bottom panels).

DISCUSSION

The consistent observations of steelhead in marine waters off of northern California were unexpected because summer marine temperatures typically exceed their marine thermal habitat preference. Investigation of the sea surface temperatures in the region revealed the presence of a cooler microclimate that may act as a thermal refuge, providing a plausible explanation for why steelhead were present, and

reinforcing just how linked steelhead marine distributions are to narrow ranges of SSTs. This microclimate appears to develop consistently each year during the summer months, disappearing by fall as temperatures warm. Steelhead were absent by September, and, while their fate remains uncertain, the timing of ocean absence by fall coincides with a life history unique to an area where immature fish return to rivers.

The regionally unique nature of the half-pounder life-history type in northern California and Kamchatka has puzzled scientists for some time, framing the two-sided perspective of what motivates these fish to behave in such a way and why it is not more common for a salmonid with the widest migratory range around the north Pacific Rim. Although limited work has been done, there appears to be no genetic divergence between individuals expressing this behavior and other fish from the same and neighboring watersheds (Busby et al. 1996; McPhee et al. 2007) and little understanding of what selective pressures might lead to this life-history type. The SSTs offshore of the Klamath region of northern California consistently provide the appropriate thermal environment ($< 14^{\circ}\text{C}$) for 1–3 months longer than other parts of the California Current. However, when this thermal refuge ultimately breaks down when fall warming encroaches on the region from all directions, remaining steelhead in the region have three options (aside from senescence): (1) travel north through surface water $> 14^{\circ}\text{C}$, (2) travel north, but move vertically to deeper, cooler water, or (3) return to a river that simultaneously is just beginning to cool from summer temperatures well above 20°C (<http://waterdata.usgs.gov/usa/nwis/uv?11530500>). We acknowledge that there is no way to confirm the samples collected in this study were fish exhibiting the half-pounder life history. Nonetheless, they provided a unique perspective to develop these hypotheses. If retreat to fresh water is purely a behavioral response to a mechanistic environmental feature, it is possible that half-pounders are not an “evolved” life history. Rather it is perhaps a fate of timing and freshwater growth for juvenile steelhead from these rivers, where fish from the same cohort, both hatchery and wild (Table 1) and possibly even family groups may diverge in life history, depending upon when they enter the ocean each spring. Further, stocks migrating past this region from the south could potentially be entrained back into these rivers. Tagging and genetics studies as well as simulation models paring movements with oceanography would be needed to address this question in the Klamath region. Additionally, while a similar temperature dynamic was observed in the Kamchatka region, the peak temperature observed there was only 12.5°C (Fig. 5). It is plausible that another mechanism exists or that being 15° farther north, these fish have a lower thermal tolerance than California stocks. Whatever the cause for this temporary return, observations that half-pounders return to sea the following spring suggests there is still a greater advantage to marine growth relative to survival/growth tradeoffs for remaining in the river.

Several Pacific salmon species including steelhead (Wurtsbaugh and Davis 1977; Welch et al. 1998b; Richter and Kolmes 2005), sockeye (*O. nerka*, Welch et al. 1998a; Eliason et al. 2011) and Chinook (*O. tshawytscha*, Hinke et al. 2005; Muñoz et al. 2015) show a thermal marine habitat preference often several degrees below optimal freshwater growth temperatures. It is speculated that they are tracking forage species associated with these regions (Atcheson et al. 2012). If diet preference for a prey with specific temperature requirements was driving this strategy, why don't steelhead evolve to pursue prey in warmer marine waters closer to their freshwater thermal optima for growth, temperatures within which far more abundant populations of Chinook salmon forage? Why do they not travel farther north into cooler waters that they are capable of tolerating to forage with even more numerous sockeye salmon? Forage niche partitioning aside, the observations of this paper and others infer strong thermal avoidance patterns that suggest a physiological mechanism.

Recent studies report warming ocean conditions may be limiting Atlantic salmon populations through top-down predation mechanisms from new warm-water predators as well as other physiological and dietary bottom-up challenges that inhibit their migration (Friedland et al. 2012; Mills et al. 2013; Friedland et al. 2014). Hayes and Kocik (2014) contrasted this with an observation that steelhead were likely buffered from such challenges by upwelling patterns in the California Current which consistently bring cool waters to the surface. However, recent warming conditions observed in the California Current call that statement into question, not just for the small region where half-pounders are observed, but for all rivers with steelhead (anadromous life histories of *O. mykiss*). Most literature regarding stressors on Pacific salmon focus on freshwater components of anthropogenic impacts and climate change scenarios (e.g., Franks and Lackey 2015; Muñoz et al. 2015). With few exceptions (Abdul-Aziz et al. 2011; Miller et al. 2014), most scientists and managers do not factor potential impacts of a shifting marine climate into harvest management or recovery planning. These would potentially include food web changes that impact fish diet, such as declines in capelin impacting Atlantic salmon stocks (Renkowitz et al. 2015). As temperature bands shift north, migrations will likely become more challenging due to increased costs associated with greater distance traveled to and from foraging grounds (Abdul-Aziz et al. 2011). In addition, shifts in timing of windows of opportunity where ocean temperatures at a river mouth are appropriate for migration could move optimal timing for smolt migration and adult return out of phase with freshwater growth and spawning cycles. This could lead to an extreme scenario in which a river is completely cut off and only freshwater life histories are possible.

The cause of extreme warm water temperature conditions in the North Pacific for 2014 and 2015, referred to as the “warm blob”, were attributed to a persistent ridge of high pressure over the Pacific Northwest (Bond et al. 2015).

While not directly linked to climate change, these high pressure ridging events may become more common in response to anthropogenic climate change (Swain et al. 2014; Diffenbaugh et al. 2015). Such conditions provide some indication for what future climate change impacts might look like in the marine environment. One observed effect of the blob was a change in the return migration routes of many sockeye around Vancouver Island from the typical 50% of the returning population rounding the south end to 99% of the return entering from the cooler north side (Gallagher 2014). Unfortunately, due to their small population numbers, limited harvest, and lack of monitoring, only a few anecdotes can be ascribed to California steelhead returns other than that they appeared to be lower than usual (unpublished data for Carmel River-Monterey Peninsula Water Management District, and Scott Creek-NMFS SWFSC). Given that they are considered to be in decline, it is difficult to say whether the warm waters observed in 2014 and 2015 can be attributed to a short-term mechanism, or possibly contribute to some longer-term decline. Salmon physiology experiments with an emphasis in aerobic scope are needed to address this question. However most of the research in this area is primarily focused upon freshwater limitations. It is time to begin expanding the investigation to the marine phase of salmon life history.

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