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SPATIAL STRUCTURE OF WATER-QUALITY IMPACTS AND FORAGING OPPORTUNITIES FOR STEELHEAD IN THE RUSSIAN RIVER ESTUARY: AN ENERGETICS PERSPECTIVE

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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
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IN THE RUSSIAN RIVER ESTUARY:
AN ENERGETICS PERSPECTIVE**

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Russian River, CA: River mouth closed



Russian River, CA: River mouth opened



Spring captured steelhead, Russian River Estuary, CA



Fall captured steelhead, Russian River Estuary, CA

Prepared for: NOAA's Habitat Blueprint ~ Russian River Habitat Focus Area, in partial fulfillment of the Russian River Habitat Focus Area Project:

Russian River Water Quality Modeling to Inform Time-Dependent Availability of Estuarine Habitat for Juvenile Salmonids

Abstract

Estuaries along the California coast are recognized as critical rearing habitat for juvenile salmonids, particularly because they provide abundant feeding opportunities that support rapid growth. However, these estuaries exhibit a high degree of spatial and temporal variability in both food availability and elements of risk such as predation risk and mediocre water quality, varying greatly in response to natural seasonal changes as well as anthropogenic effects and management. Physical models—such as a quantified conceptual model (QCM) developed by UC Davis for the Russian River Estuary—can be used to predict the spatially explicit response of Estuary water quality and quantity to seasonal change and management interventions. These predictions take the form of depth-profiles of temperature, dissolved oxygen and salinity throughout the Estuary, calibrated to sonde measurements collected as part of regular monitoring. To aid in the interpretation of the outputs of such models, here we synthesize a categorical rating scheme for how water quality and spatial location in the Estuary affects rearing steelhead in terms of foraging opportunity, predation risk, and physiological impacts of water quality. We adopt a bioenergetics perspective as a conceptual framework because energy provides a unifying framework for thinking about how behavioral and physiological responses to predation risk, water quality, and foraging opportunity translate to somatic growth of rearing salmonids. However, our review and synthesis indicates that the tradeoffs posed to rearing salmonids by an estuary—among foraging opportunities and the different dimensions of water-quality impacts, for example—is multidimensional and complex. Rather than propose explicit quantitative models of behavior and physiology that capture all this complexity—which is outside our scope and in any case requires further work—for simplicity we develop a categorical (or qualitative) scheme to make sense of this complexity. It is our hope that this scheme will aid fisheries managers in interpreting the complex output of physical estuary models, and point the way toward more focused development of coupled behavioral-bioenergetics models of salmonids rearing in estuaries. Such models will need to address the spatial and temporal structure of the tradeoffs, as well as the important role of induced physiological tolerance for salinity and possibly hypoxic conditions, and its relationship to strategies for feeding, growth efficiency, and predator avoidance. For convenience the qualitative rating scheme is summarized in a short appendix at the end of the text.

Introduction

In the Mediterranean-type climate of California, estuaries are recognized as critical habitat for juveniles¹ of many salmonid species. These estuaries exhibit a high degree of variability in both abiotic parameters and food availability – responding to natural seasonal changes as well as anthropogenic effects and management. Quantitative measures of habitat availability in time and space are needed to identify key factors influencing habitat conditions favorable to juvenile salmonids. Such measures would aid in identifying those management options that promote estuarine conditions beneficial to imperiled salmonid populations.

The University of California, Davis Bodega Marine Laboratory (BML) has developed a conceptual approach for quantifying the volume of salmonid estuarine habitats as a function of river inflow (discharge, temperature) and state of the estuary mouth (fully open, fully closed, perched). This “quantified conceptual model” (QCM) is a simple modeling approach that combines estuary bathymetry; empirical time-series on water level and depth-profiles of water quality parameters; a lagoon water balance; and a parametric model of the mouth and beach (Behrens et al. 2015). Salmonid habitats are characterized in terms of water quality metrics (*i.e.*, temperature, dissolved oxygen, salinity) indexed by spatial location in the estuary and depth below the current water level. The QCM developed for the Russian River Estuary can provide managers with a real-time, empirically based, spatiotemporal decision support tool for assessing the quantity and quality of juvenile salmonid habitat that is likely to result from various river mouth conditions. However, the output of the QCM is not in terms of salmonid habitat per se, but in terms of spatially explicit predictions for depth profiles of temperature, dissolved oxygen and salinity throughout the estuary, which can be summarized as total volumes of habitat with specific combinations of the water quality parameters and depths (distance from water surface, distance from estuary bottom). To close the gap between model outputs and predicted implications for salmonids, a team of fisheries and estuarine ecologists was assembled to develop a categorical rating scheme for evaluating outputs from the QCM. The rating scheme is developed in this Technical Memorandum based on a literature review and data on juvenile salmonid habitat use and invertebrate distribution in the Russian River Estuary. We also identify ways in which our simple categorical rating scheme is likely to be inadequate relative to fully-developed quantitative models of salmonid bioenergetics and behavior.

Juvenile salmonid water-quality preferences and tolerances vary by species. Additionally, the degree to which juveniles of a given species rely on estuarine habitat are influenced by spatiotemporal factors that can lead to short-term shifts in life history strategies, such as extended estuarine-rearing, as well as longer-term local adaptation. Although we recognize the potential importance of the estuary to juvenile coho and Chinook salmon, for clarity we focus this technical memorandum on steelhead occupying the estuary. However, the framework we describe here could serve as a template for future efforts that is populated with species-specific WQ and depth values to consider estuarine habitat conditions for juvenile coho and Chinook as they relate to inlet conditions.

¹ We define the term juvenile as exogenous-feeding life stages prior to ocean entry; therefore, individuals that mature prior to the smolt stage (*e.g.*, precocious males) are included in this definition.

Background

Since 2004, Sonoma County Water Agency (SCWA) has continuously monitored water temperature, dissolved oxygen (DO), pH, salinity, and depth using datasondes deployed in the lower [0 - 1.7 river kilometer (rkm)], middle (1.7 - 5.0 rkm), and upper (5.0 - 12.0 rkm) reaches of the estuary (Brown's Riffle to the river mouth). The National Marine Fisheries Service's (NMFS) Russian River Biological Opinion (2008) requires SCWA to continue monitoring these water-quality parameters under changing estuary conditions during the lagoon management season (May 15 to October 15) and to evaluate changes in these water-quality parameters that result from lagoon adaptive management (*i.e.*, managing the estuary as a seasonal lagoon). However, SCWA is not required to provide additional synthesis and/or modeling of past, current, or future WQ data collected. Independent of regulatory requirements, NOAA has partnered with SCWA via the Russian River Habitat Focus Area, who has contracted with BML for collection and evaluation of data relating to estuarine hydrodynamics, water quality, and physical processes associated with river mouth conditions. SCWA has also contracted with Environmental Science Associates (ESA) and BML for the development of a FLOW3D model of water circulation and stratification that utilizes the water quality data collected by BML and SCWA.

Purpose of this Technical Memorandum

The water quality parameters used to inform habitat availability and productivity for juvenile salmonids in the estuary include temperature ($^{\circ}$ C), DO (mg/L), and salinity (‰). Suboptimal levels of these water quality parameters involve increased energy expenditure, slower growth, and eventually mortality at extreme levels, as indicated in the categorical rating scheme developed below and used to interpret the QCM outputs in terms consequences for rearing juvenile steelhead. However, the productivity and juvenile salmonid growth potential of available habitat involves complex interactions, such as higher oxygen demand at higher water temperatures or salinities that cannot be fully captured by a categorical rating scheme. Therefore, we have provided this technical memorandum to explain and support the rationale for each rating scheme, the complexities of salmonid physiology, bioenergetics and behavior, and the subsequent limitations of the modeling outputs and recommendations to address them (*e.g.*, bioenergetics models, partial life history model, *etc.*).

Additionally, water depth (m) is an output of the QCM and will be used to evaluate juvenile salmonid foraging opportunities, prey availability and predation risk that tend to be structured by water depth and characteristics of the benthic substrate. Water depth considerations also include tradeoffs between foraging opportunities (*i.e.*, location of prey availability) both vertically in the water column and horizontally across the width of the estuary in relation to potential avian and aquatic predation risk.



Figure 1. Example of a suspected freshwater-acclimated resident steelhead captured in the Russian River Estuary, CA.



Figure 2. Example of a suspected marine-acclimated resident steelhead captured the in the Russian River Estuary, CA.



A. PIT # B4E, captured 8/13/2012, 134 mm FL, Russian River Estuary at Jenner Gulch, CA.



B. PIT # B4E, re-captured 9/24/2012, 185 mm FL, Russian River Estuary at Jenner Gulch, CA.



C. PIT # B4E, recaptured 10/15/2012, 209 mm FL, Russian River Estuary at Jenner Gulch, CA.

Figure 3. Example of a juvenile steelhead captured and subsequently re-captured in a stratified brackish to full strength seawater environment (mouth of Jenner Gulch, CA). Actual saltwater tolerances are unknown; however, this example portrays the potential range of some individuals to increase their capacity to excrete salt ions while continuing to grow.

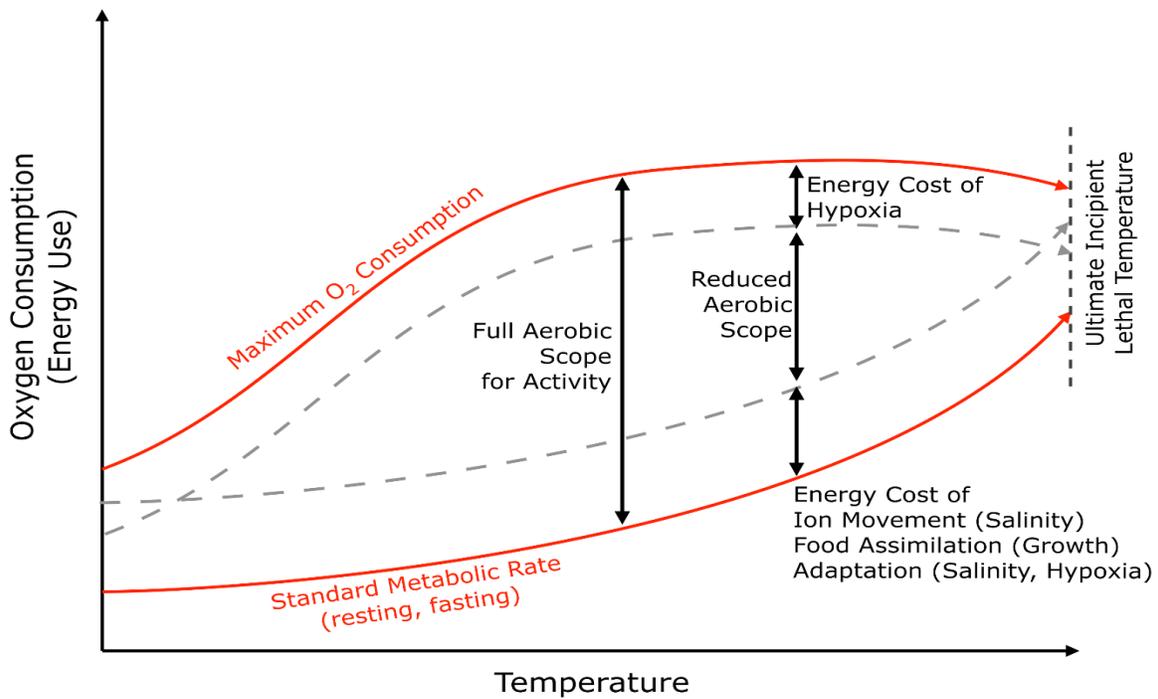


Figure 4. Schematic model of energetic costs of temperature, salinity and hypoxia for fishes, adapted from Farrell (2009) and Wang et al. (2009).

Life Stage Categories

Two juvenile steelhead life stage categories and their water quality tolerances have been selected to inform the water quality habitat and productivity components within the estuary during the dry season (generally spring through fall). We considered both categories as encompassing juveniles that rear in the estuary. Therefore, we did not focus on smolts² because they theoretically do not rear in the estuary, but instead spend a relatively brief period migrating through the estuary during a time (majority before June) when water quality conditions are generally suitable for salmonids that can tolerate full strength seawater.

1. **Freshwater-Acclimated Residents:** Individuals that rear in the estuary prior to smoltification, but are limited in their capacity to osmoregulate in seawater. These individuals may increase their capacity to excrete salt ions over time and therefore become fully marine-acclimated residents (Figures 1 and 3).
2. **Marine-Acclimated Residents:** Individuals that rear in the estuary prior to smoltification and have the capacity to osmoregulate in full strength seawater (Figures 2 and 3).

² We define the term smolt as juvenile salmonids that have gone through the parr-smolt transformation (*i.e.*, smoltification) via a suite of behavioral, morphological, and physiological changes as they migrate directly to sea for the first time (McCormick 2013). This downstream seaward migration generally occurs before June in the Russian River, CA.

Water Quality Tolerances for Juvenile Pacific Salmonids, an Energetics Perspective

From an evolutionary perspective, fish are a device to convert food energy and mass into more fish, via growth and reproduction. However, in doing so a fish incurs energetic “overhead:” energy used to maintain the living body and assimilate food in order to support adaptive behaviors such as feeding and predator avoidance; and, to support the energy cost of adaptive physiological responses to stressful environments. The ability of a fish to perform these functions is limited by the energy content of food, as well as the supply of oxygen available for converting food to energy via respiration. One way of conceptualizing these processes is the concept of *aerobic scope*, the difference between standard metabolic rate—the level of respiration necessary to maintain a fish at rest—and maximum metabolic rate, usually determined by the maximum capacity of the gills to absorb oxygen from the water or the maximum capacity of the heart to transport oxygen in the blood (Figure 4). Aerobic scope—sometimes called “scope for activity”—describes the power³ available to the fish for life functions other than maintenance, and it is useful to categorize these functions in terms of evolutionary fitness: feeding, avoiding predation, food assimilation (*i.e.*, converting food into body mass and eggs), and mitigating physiological costs such as suboptimal water quality.

Poor water quality may incur energetic costs that reduce the aerobic scope significantly (Figure 4); yet, it still can be adaptive for a fish to move into poor water if the benefits of feeding, assimilation efficiency or predator avoidance outweigh the energetic costs of poor water quality. However, if aerobic scope is reduced too much there may be insufficient power to pursue behaviors such as feeding, or even to support the energy cost of food assimilation and growth. In this manner, energy provides a scientifically sound common currency for thinking about how evolution should adaptively structure the tradeoffs that fish experience between foraging opportunity, predation risk, and the cost of inhabiting poor water conditions. Normally functioning ecosystems may seldom provide fish with a habitat that is simultaneously optimal on all three axes, producing a selection pressure favoring fish that can evaluate and respond adaptively to the energetic tradeoffs presented by different available habitats over time. If these adaptive behaviors and physiological responses can be quantified and modeled, they would provide a predictive tool for how juvenile salmonids would have the opportunity to respond to novel habitat conditions, and thus could be a useful tool for habitat management.

The following is a review of the underlying physiological mechanisms and energetic considerations associated with three aspects of water quality relevant to salmonid fishes: water temperature, salinity, and DO. Additionally, field studies and lab experiments were reviewed on how fish respond behaviorally (*e.g.*, movement, foraging, and habitat use) to energetic tradeoffs involving water quality, occurrence of predators, and food availability.

Upper Thermal Limits of Steelhead

Upper temperature limits for survival of steelhead and rainbow trout (*i.e.*, anadromous and non-anadromous, *Oncorhynchus mykiss*, respectively) and other fish are estimated in the laboratory as either the Critical Thermal Maximum (CTM) or Incipient Lethal Temperature (ILT). CTM is the temperature at which fish lose ability to maintain upright posture after short exposure, taken to indicate impending death; ILT is the temperature for which long exposure produces 50%

³ “power” here is the *rate* at which energy can be used, *i.e.* transformed to some other form of energy such as muscle movement.

mortality, and is assumed to be less than CTM (Jobling 1981). Estimates of both vary widely in literature reviews. Hasnain et al. (2013) found mean ILT for juvenile steelhead was 25° C [standard deviation (SD), 2.3° C] across studies from Canada and the northern USA; mean CTM was 22.1° C (SD, 6.5° C). Notice that mean ILT was greater than mean CTM, contrary to expectation, and SD of CTM across studies was rather wide (6.5° C). Myrick and Cech (2004) found estimates of ILT ranging from 22.8° C to 26° C. Steelhead from the American River (California) had CTMs of 27.5° C to 29.6° C depending on acclimation; and steelhead juveniles from the Feather River (California) had CTM of 30.8° C, considerably higher than the mean values in Hasnain et al. (2013). Bjorn and Reiser (1991) reported studies showing juvenile steelhead CTM of 29.4° C and ILT of 25° C. More recently, redband trout (*O. mykiss*) were found to have CTM of 29.4° C in southeast Oregon, leading Rodnick et al. (2004) to suggest that physiological mechanisms for CTM are highly conserved evolutionarily, but question its use as suitability criterion because other metabolic traits were more population-specific. Some variation in CTM may be due to variation in laboratory methods. For example, the acclimation temperature at which the fish is held prior to the experiment, and the rate at which temperature is increases can both strongly affect estimates of CTM. In a sense, CTM is not a true biological trait, but rather a hybrid trait that is determined by both the biology of the tested individuals and the experimental protocol.

Studies of the regional distribution of wild steelhead and rainbow trout have generally shown the species to occur over a broad thermal range. Dunham et al. (2007) found steelhead occurred over the full range of observed maximum daily stream temperatures (11.7° - 26.6° C) in the Boise River Basin, Idaho. Huff et al. (2005) observed steelhead at the warmest site in each ecoregion of Oregon they studied, up to the maximum observed temperature of 28.6° C (7-day average daily maximum) (see their Table 1). Redband trout in southwestern Idaho were observed in water with maximum temperatures ranging between 25.5° C and 29° C, but not in a downstream area with suitable habitat and flow but maximum temperatures > 29° C (Zoellick 1999). These studies did not ask if thermal refugia were available to the fish.

Under warm river temperatures, steelhead and rainbow trout often use thermal refugia if they are available. In a northern California creek, two-thirds of steelhead moved into thermally-stratified pools when ambient stream temperature rose into the range 23° - 28° C (Nielsen et al. 1994). In a nearby river, summer-run adult steelhead used stratified pools over the entire observed range of river temperatures 26° - 29° C, and pool bottoms were 3.5° cooler. In northeast Oregon, proportional use of thermal refugia rapidly increased when temperatures rose from below 21° to above 22° C mean daily maximum temperature (Ebersole et al. 2001), although nonzero densities were observed over the full range of observed temperatures (15.7° - 25.1° C mean daily maximum). Comparing river reaches with different amounts of cold-water habitat area, Ebersole et al. (2003) estimated that steelhead density in reaches increased only 10% with each doubling of cold-water patch area, rather than proportionately. This suggests that fish from a broader surrounding area crowd into pools as necessary, rather than that cold-water area strictly controls fish densities via territorial interactions within the cold-water patch. In the mainstem Klamath River (northern California), the occurrence of steelhead in thermal refugia increased above river temperatures of 22° - 23° C (Sutton et al. 2007). In late summer in tributaries of the Salinas River (Central California), steelhead were only observed in pools where mean water temperature stayed below 21.5° C and maximum temperature stayed below 26° C, presumably because most

fish moved to cooler areas upstream (Thompson et al. 2012). In Sespe Creek (southern California), steelhead concentrated in sections of stratified pools with mean daytime temperatures $< 20^{\circ}\text{C}$, when mean daytime temperatures elsewhere were $20^{\circ} - 20.7^{\circ}\text{C}$ (Matthews and Berg 1997).

Although steelhead and rainbow trout often use thermal refugia, it is not a universal behavior. In stratified pools in a Sierra Nevada stream, rainbow trout used temperatures up to 19.3°C (maximum temperature observed) even when cooler water was available (14.5°C), providing no evidence that trout selected the cooler water (Matthews et al. 1994). A few studies in southern California have shown that steelhead can persist at higher temperatures without the availability of thermal refugia. Spina (2007) found a lack of thermal refugia in a section of Topanga Creek (Santa Monica Mountains) occupied by steelhead, which presumably prevented the fish from behavioral thermoregulation when the creek ranged between 17.4° and 24.8°C over time. In Santa Paula Creek (Transverse Ranges), thermal refugia were rare and yet steelhead persisted in all pools that did not exceed 30°C maximum temperature, with a sharp threshold of elimination above 30° ; however, feeding and agonistic behavior declined above $\sim 24^{\circ}\text{C}$, presumably due to thermal stress (Sloat and Osterback 2013). For steelhead, Werner et al. (2005) found that the heat shock protein hsp72 of steelhead from northern California river, was induced by 25°C water in lab; in the river, they observed hsp72 in fish collected during conditions of $18^{\circ} - 19^{\circ}\text{C}$ mean daily temperature, or $20^{\circ} - 22.5^{\circ}\text{C}$ mean daily maximum.

The above body of work suggests that steelhead can persist in streams provided that short-term maximum temperatures remain below 30°C or perhaps 29°C (Zoellick 1999; Rodnick et al. 2004; Werner et al. 2005; Sloat and Osterback 2013), similar to laboratory estimates of CTM. However, above $22^{\circ} - 24^{\circ}\text{C}$, feeding and agonistic behavior falls off (Sloat and Osterback 2013) and fish show signs of stress (Werner et al. 2005). Estimates of ILT (50% mortality after long exposure) vary across studies but tend toward 25°C . If thermal refugia are available, steelhead start to concentrate in them when temperatures exceed 21°C and almost completely retreat at temperatures around 24°C (Nielsen et al. 1994; Ebersole et al. 2001; Baird and Krueger 2003). Many streams in southern California that support steelhead do not provide such refugia, and steelhead actively feed in the presumably stressful temperature range of $21^{\circ} - 24^{\circ}\text{C}$ (Spina 2007; Sloat and Osterback 2013).

These findings suggest various temperature thresholds for steelhead that can summarize, at least to some degree, the underlying physiological and behavioral adaptations that shape species fitness at high temperatures. Here we assume three biological indicators: A day is *thermally suitable* if maximum daily temperature stays below 29°C and mean daily temperature stays below 25°C . In this usage suitability means that temperature will not necessarily kill fish over a short time period (hours to days), but the fish will not necessarily thrive and may be quite stressed or unable to devote food energy to growth or reproduction. We therefore additionally quantify thermal stress based on evidence of behavioral thermoregulation or physiological stress from our literature review: A day is *thermally stressful* if temperature rises above 21°C at any time, with the *stress intensity* quantified as degree-hours above 21°C [*i.e.* for each day, $\sum(T_i - 21)\Delta t$].

Thermal Growth Potential

Thermal growth potential is the maximum attainable growth of an individual fish as a function of the river's or estuary's thermal regime under an actual or constructed scenario of temperature and food availability. Thermal growth potential can be estimated using the bioenergetics model for steelhead, as described by Railsback and Rose (1999) and modified by Satterthwaite et al. (2010) and Arriaza (2013). This model is parameterized from results of standard laboratory respirometry studies on *O. mykiss* (Railsback and Rose 1999) in which ambient DO levels are close to saturation. Individual growth arises from the surplus between energy intake and energy expenditure (Rand et al. 1993; Railsback and Rose 1999; Satterthwaite et al. 2010), modeled as weight- and temperature-dependent functions for food consumption and respiration respectively. For weight W , growth rate is the difference

$$(1) \quad \frac{dW}{dt} = \Psi(T(t))fcW(t)^{0.86} \frac{a(t)}{\kappa(t)+a(t)} - (1 + a(t))W(t)\alpha e^{0.071 \cdot T(t)}$$

where the first and second terms describe energy intake and expenditure, respectively. In the intake term, $\Psi(T(t))fcW(t)^{0.86}$ describes maximum food consumption, composed of two functions and empirical scaling parameters. The function $W(t)^{0.86}$ is an empirical allometric relationship between maximum consumption and fish weight at time t . The function $\Psi(T(t))$ is a relationship between maximum consumption and temperature T at time t . The functional form of $\Psi(T(t))$ is hump-shaped for cold-water species, after Thornton and Lessem (1978), parameterized for California steelhead as in Railsback and Rose (1999). These functions are scaled by two constants: f , the relative energy density of food to fish tissue; and, c , the daily maximum weight of food that can be consumed by a 1 g fish under optimal temperature.

The expenditure term involves fish weight $W(t)$, a standard unit catabolic cost α , and an effect of temperature in catabolism, $e^{0.071T(t)}$ (Brett and Groves 1979). Parameters c , f , and α have been previously estimated for California steelhead (Central Valley) from laboratory studies (Rao 1968; 1971; Myrick 1998; Railsback and Rose 1999; Satterthwaite et al. 2010).

To appropriately characterize fish growth in the wild, these expressions for maximum food intake and respiration costs were scaled by two additional functions, energy cost of activity $a(t)$ and difficulty of finding food $\kappa(t)$, in accordance with recommended practices by Andersen and Riis-Vestergaard (2004) and Bajer et al. (2004). While higher activity increases consumption, total energetic cost also goes up. Here we assume that fish choose a unique activity level, $a^*(t)$, that optimizes growth given all other parameters. Differentiating (1) with respect to $a(t)$ and solving gives growth-optimized activity

$$(2) \quad a^*(t) = \sqrt{\frac{\kappa(t)\Psi(T(t))fcW(t)^{0.86}}{W(t)\alpha e^{0.071 \cdot T(t)}}} - \kappa(t)$$

at time t . In the resulting model, growth rate depends on fish size and food availability, but generally peaks in the range 15° - 17° C and becomes negative above 22° - 24° C.

Based on the above information, the following temperature (° C) rating scheme was used for freshwater- and marine-acclimated residents (Table 1; Appendix A):

Table 1. Temperature (° C) rating scheme for freshwater- and marine-acclimated residents.

Fastest growth	Positive growth	No or Negative growth	Unsuitable
14° - 18° C	< 14° or 18° - 21° C	21° - 25° C	> 25° C

Definitions:

Fastest growth: Temperature conditions that allow for the most rapid growth when food availability is unlimited.

Positive growth: Temperature conditions that allow for positive growth (weight gain) under most levels of DO, salinity, and food availability.

No or negative growth: Temperature conditions that usually produce high metabolic demand and negative growth (weight loss) even when food is readily available.

Unsuitable: Temperature conditions that are highly stressful and generally cannot sustain metabolic demand for more than a day without death or injury.

Salinity Tolerance

Tolerance for salinity derives from a fish's ability to maintain non-equilibrium salinity gradients between their blood plasma and the external water column, a form of homeostasis. Blood plasma typically has salinity around 8 - 10 ‰ whereas full-strength seawater is 30 ‰, that together drive a net diffusion of dissolved ions into the fish (toward the lower ionic concentration) and net diffusion of water the other way, out of the fish. Without a physiological mechanism to pump ions and/or water backwards against these concentration gradients, fish blood would become progressively saltier until it equilibrates with seawater, causing mortality. In fresh water, the gradients are reversed and fish tend to lose ions and gain water from their environment, diluting their blood past lethal limits in the other direction. Tolerance thus involves the maintenance of the internal milieu via physiological mechanisms that transport ions and/or water molecules from areas of low concentration to high concentration, a process that requires energy and regulation (McCormick 2013).

In principal, there is an isotonic environment around 8-10 ‰ in which external salinity matches internal salinity and no such active transport of ions or water need occur; at lower salinities fish need to actively import ions or export water to survive; at higher salinities, they must actively export ions and conserve water molecules (Morgan and Iwama 1991; Ern et al. 2014). In fact, Fu et al. (2010) argue that the initial function of gills in small larval rainbow trout is ion exchange rather than gas exchange.

Thus, we expect a fish in fresh water to express modest salinity tolerance (up to the isotonic point), simply by down-regulating its uptake of ions and export of water. But past the isotonic point, tolerance requires a qualitatively different ability to actively export ions and retain water. Anadromous salmonids typically develop this ability during a physiological transition known as smoltification, in which freshwater juvenile salmonids transform into a migratory form via changes in morphology, body coloration, swimming behavior, and saltwater tolerance. Saltwater tolerance develops prior to any exposure to salt water by way of hormone-triggered build-up of certain gill proteins that move Na⁺ and K⁺ ions across the gill from plasma to seawater (McCormick 2013). Other gill proteins and channel structures also develop that allow chloride (Cl⁻) ions to passively follow the gradients set up by the active transport of Na⁺ and K⁺.

McCormick (1993) developed a non-lethal gill biopsy procedure, Na⁺ K⁺ ATPase (NKA), to measure the activity of the main protein involved in salinity tolerance and this biopsy procedure is now commonly used as an indicator of salinity tolerance in salmonids. NKA hydrolyzes the energy-bearing molecule adenosine triphosphate (ATP) that in the process uses the energy to transport Na⁺ and K⁺ ions against concentration gradients across the gill lamellae. Gills actually contain two isoforms of the molecule, known as NKA α 1a and NKA α 1b that are associated with freshwater tolerance (ion importing) and salinity-tolerance (ion exporting), respectively (McCormick 2001; Flores and Shrimpton 2012). In salmonids, the stress hormone cortisol plus growth hormone appears to stimulate production of NKA α 1b, raising salinity tolerance; whereas, cortisol plus the hormone prolactin appears to stimulate production of NKA α 1a and increasing freshwater tolerance (McCormick 2001; Flores and Shrimpton 2012). Thus, growth hormone and prolactin drive antagonistic interpretations of a cortisol increase. The biopsy procedure of McCormick (1993) does not distinguish between the two isoforms. However, the concentration of NKA α 1b in saltwater-acclimated salmonids tends to be substantially greater than the concentration NKA α 1a in freshwater-acclimated salmonids, perhaps because saltwater-acclimated fish are further from the isotonic point than freshwater-acclimated fish (Flores and Shrimpton 2012). Thus, total NKA activity can still function as “bulk” indicator of saltwater tolerance, with higher levels of activity generally indicating greater capacity to use metabolic energy (via ATP) to actively exports ions from the gills.

Smoltification vs. Induced Salinity Tolerance

The development of salinity tolerance during smoltification is anticipatory: it occurs while the fish is still in fresh water (McCormick 2013) and downstream migrants thus have elevated NKA activity prior to exposure to salt water (Hayes et al. 2012). It appears to be triggered by changes in photoperiod (Handeland and Stefansson 2002), conditional on the individual having grown to a threshold body size suitable for surviving in the ocean (Satterthwaite et al. 2009; Beakes et al. 2010). Downstream migration in anadromous salmonids is generally highly seasonal but varies among species and among geographic regions within species (Spence and Hall 2010), probably as a result of selective factors (niche differentiation and local adaptation, respectively). As such, the combination of threshold body size and photoperiod makes evolutionary sense as reliable cues, in which the precise day-length and body size that cues smoltification could be adjusted to local conditions by natural selection. Other environmental factors such as temperature, stream flow and lunar phase appear to combine with photoperiod to cue the timing of downstream migration after smoltification (Spence and Dick 2014).

Salinity tolerance can also be directly induced by exposure to salt water, a distinctly different cuing system than the anticipatory tolerance of smolts. Flores and Shrimpton (2012) introduced rainbow trout to 24 ‰ salt water (75% of full-strength seawater) and after 14 days found an increase in gill NKA activity, higher expression of mRNA for the α 1b isoform of NKA, and changes in levels of the cuing hormones cortisol, growth hormone and prolactin that were similar to what is observed during smoltification (*e.g.*, McCormick 2013). Perry et al. (2006) conducted an experiment in which salt was added to the diet of experimental rainbow trout but not controls, both kept in fresh water. They found that gill NKA activity was 1.5 in controls, but 3.5 in fish with the high-salt diet. They also observed other biochemical and cellular changes consistent with salt-water gill structure. However, two elements of the saltwater phenotype were not observed: the disappearance of mitochondrial-rich cells from the gill lamellae and the development of “leaky junctions” between chloride cells and accessory cells.

Fuentes et al. (1996) found that the exposure of small (40 g) rainbow trout to isotonic (9 ‰) and seawater (28 ‰) induced greater NKA activity in the kidneys, but did not observe such a response in larger (180 g) fish. This suggests that kidneys can also be induced to regulate ions and that larger fish may be somehow more resistant to such induction, perhaps because larger body masses imply large volumes of plasma relative to ion intake.

Thus, exposure to salt water and consumption of salt both appear to directly induce the gills to develop salinity tolerance. Exposure to salt also induces ion regulation within the kidneys. The time-scale of such induction appears to be on the order of two to three weeks, but may vary more widely according to size of fish and other factors. Importantly, the literature is not clear on whether *Oncorhynchus* spp. can be directly induced to tolerate full-strength seawater. In their experiments, Flores and Shrimpton (2012) used 75% strength seawater, because “higher salinity levels can cause mortality,” but they provide no data.

Energetic Costs of Salinity Tolerance

The active transport of ions across the gill membrane consumes metabolic energy, and the retooling of gill proteins during smoltification or direct induction presumably entails energetic “start-up” costs as well. Energy can be thought of as an internal currency that is allocated by the organism to capture food (additional energy) and convert it into survival, growth and reproduction via behavioral and physiological mechanisms (Sousa et al. 2010). Thus, it is worth knowing something about the magnitude of energetic costs for salinity tolerance, because this will give an idea of the situations in which it is adaptive for a species to volitionally enter salt water, self-induce tolerance, incur an energy cost, but presumably still benefit in some way due to better feeding opportunities (Webster and Dill 2006).

Scientific reviews (Morgan and Iwama 1991; Ern et al. 2014) of a broad array of fish taxa expected to find that the lowest energy costs were in isotonic salinities, for the reasons described earlier. They found this in some species but overall a more diverse and complex picture suggested that lowest energy costs were often for marine-fish in salt water and freshwater fish in fresh water. This suggests selective pressure for energy efficiency in the native habitat rather than natural energy efficiency at the isotonic point. However, there were many exceptions and it is possible that acclimation costs (“start-up costs”) were not distinguished from the longer-term costs of maintaining plasma ion levels, and probably also from costs of various miscellaneous physiological responses to salinity.

Morgan and Iwama (1991) acclimated fry of resident *O. mykiss*, anadromous *O. mykiss*, and *O. tshawytscha* to a range of salinities, while providing equal food availability across all treatments. Survival, growth, metabolic rate, plasma Na⁺ and Cl⁻ concentrations, and seawater adaptability were measured for 5 - 12 weeks, depending on the species. Growth of all three taxa was highest in fresh water and declined with increasing salinity. Metabolic rates increased with salinity and were inversely correlated with growth rates. Isotonic salinity did not offer significant metabolic or growth advantages to any of the fry. While plasma Na⁺ and Cl⁻ concentrations varied among groups, *O. tshawytscha* fry tended to better maintain ionic homeostasis at higher salinities than the *O. mykiss*. Acclimation to the various dilute salinities did not influence the seawater adaptability of anadromous *O. mykiss* or *O. tshawytscha*. The results suggested that energetic cost of ion regulation increased with salinity and were sufficient to affect growth. However, attempts to quantify the cost were probably affected by additional metabolic processes that responded to salinity.

Morgan and Iwama (1998) conducted similar experiments on juvenile *O. kisutch* in three treatments: acclimated to fresh water, isotonic salinity (10 ‰) and full-strength seawater (28 ‰). Plasma levels of cortisol, glucose and ions (Na⁺, K⁺, Cl⁻), gill NKA activity, and oxygen consumption were sampled for six weeks. Following an initial adjustment period, plasma constituents in saltwater coho returned to near-freshwater values, indicating that the coho were acclimated to salt water by day 21. NKA activities on days 21 and 42 were lowest in isotonic water, higher in fresh water and highest in salt water. This result is consistent with the idea that less energy would be required to maintain ion balance in isotonic environments, and that salt water requires more energy expenditure on ion transport than fresh water. However, swimming coho (one body length per second) had similar oxygen consumption across the three test salinities after six weeks, suggesting that modest activity masks the costs of maintenance, at least in the presence of error levels typical of respirometry studies.

Morgan and Iwama (1999) estimated oxygen consumption in excised gill tissue of fresh water-adapted cutthroat trout (*O. clarki clarki*) with and without inhibitors of Na⁺/K⁺/H⁺ pumps. They estimated that these pumps accounted for 37% of total tissue respiration in fresh water-adapted gill tissue, and 1.8% of whole-animal oxygen consumption. Oxygen consumption of fresh water-adapted tissue was 33% higher than in seawater-adapted tissue. They estimated that total gill oxygen consumption accounted for 3.9% of resting metabolic rate in fresh water-adapted trout and 2.4% of seawater-adapted trout.

Maxime (2002) introduced juvenile Atlantic salmon (*Salmo salar*) to salt water at various points during the parr-smolt transition and found that the standard metabolic rate increased during that time. Prior to the transition, salt water actually decreased the standard metabolic rate, possibly due to effects of increased plasma-ions on gas exchange in the gills or oxygen affinity of hemoglobin.

Altinok and Grizzle (2001) found that juvenile *O. mykiss* (< 0.5 yr) in modest salinities (3 and 9 ‰) had higher specific growth rate and more efficient food conversion and energy absorption than in lower salinities (fresh water and 1 ‰), supporting the idea that costs go down near the isotonic point. Handeland and Stefansson (2002) conducted an experiment on Atlantic salmon (*S. salar*) pre-smolts in which they phase-advanced photoperiod followed some weeks later by transfer from fresh water to various salinities. They found that hypo-osmoregulatory ability improved in all groups during the first nine weeks of the photoperiod treatment, and that salinity was probably not necessary to stimulate hypo-osmoregulatory ability, but did have a negative effect (13% decrease) on post-smolt growth. Thus, the energy cost of salinity tolerance in smolts appears sufficient to affect growth, suggesting that tradeoffs between benefits of food availability and costs of saltwater tolerance would be of comparable magnitude in ecological situations.

Ecological Implications, Possible Indicators

In a non-migratory ecological setting where juveniles have the opportunity but not the necessity to use saltwater habitats, natural selection is only expected to favor movement and acclimation to salt water if the energetic cost is somehow offset by some gain, such as increased feeding ability (energy intake), more suitable temperatures (which affect metabolic rate and growth conversion efficiency), or realization of some other habitat preference such as water depths that are presumably defensive against predators (Webster and Dill 2006; 2007; Webster et al. 2007).

For example, Webster and Dill (2006) used salmonid habitat choice experiments, and in particular a “behavioral titration,” to ask how juvenile *O. tshawytscha* respond to energetic tradeoffs between food availability and water temperature or water salinity. Age-0 salmon of size $70.2 + 8.2$ mm (temperature trials) or $88.7 + 3.1$ mm (salinity trials) were found to prefer brackish (15 ‰) and salt (27 ‰) water over fresh water. Food availability was increased in fresh water to determine if the strength of preference was explained purely by lower energetic costs in brackish and salt water, and this hypothesis was supported for brackish but only partially supported for full saltwater treatment. In addition, NKA activity increased in juvenile Chinook over the course of the experiment, but not in the brackish treatment. Webster and Dill (2006) interpreted this to mean that fish were isotonic to brackish water and no NKA response was elicited, whereas salt water elicited a continuous increase in gill NKA over the course of the experiment. They also concluded that energetic costs of non-preferred water temperatures (14° C vs. 9° C) were of similar magnitude as energetic costs of non-preferred salinities (fresh water and salt water versus preferred brackish water). This behavioral-titration method could have broad application for determining how fish volitionally enter habitats to trade-off the costs of salinity tolerance versus benefits of saltwater use, such as access to greater depths (protection from predators) in stratified freshwater-saltwater systems (Webster et al. 2007). It assumes such behavior reflects adaptive preferences within the local ecological niche space used by the species.

Hayes et al. (2012) observed juvenile *O. mykiss* moving downstream with elevated NKA levels (relative to non-movers) during all months of the year. The highest NKA levels were observed during smolting season (Apr-May), but elevated NKA levels were also observed in the summer and fall when further downstream access to the ocean was blocked by a seasonal sand-bar barrier. These juvenile *O. mykiss* moving downstream outside of the smolting season generally had NKA levels intermediate to smolts and non-moving juveniles, and subsequently resided in the estuary where heterogeneous salinities ranging between fresh and full strength seawater could be found. This suggests perhaps that the smoltification/induced-tolerance dichotomy, outlined earlier, is not the whole story.

Generally, while commonly observed and consistent with physiological studies of induced tolerance, the volitional entry of juvenile salmonids into brackish and sea water in the wild has actually received very little attention in the ecological literature. A notable exception is the work by Webster and Dill cited above, that conceives volitional movement between salt and fresh water as a laboratory choice experiment. This and other work suggests that salinity poses some level of stress on juvenile salmonids, triggering higher levels of the stress hormone cortisol, that in turn induces a remodeling of the gill physiology to actively export ions. Thus, stress for a juvenile salmonids in a saline habitat is not necessarily an indicator of poor habitat but rather a trigger for physiological adaptation to that habitat. The cost of such adaptation is simply energy and thus the habitat might actually be considered high-quality from the point of view of evolution if its benefits (food availability, safety from predators, etc.) outweigh the energy cost of induced tolerance.

For juveniles (not yet smolted) of the various species of *Oncorhynchus*, the above review suggests there are four energetic categories of salinity (Figure 5; Table 2): (1) hypotonic (< 10 ‰), used by juvenile salmonids in which the ion-importing pumps of the gill are available; (2) isotonic (10 – 15 ‰), available to all juvenile salmonids; (3) hypertonic (15 – 28 ‰), available to juvenile salmonids in which the ion-exporting pumps have been induced; and, (4)

marine (> 28 ‰), which may be too salty for indefinite use of juvenile salmonids with induced tolerance. Note that this last category includes full-strength seawater. This categorization is too simplistic in a number of ways:

- 1) It is really unclear whether the threshold for unsuitable should be as low as 28 ‰, or in other words, whether juvenile salmonids can be directly induced to physiologically adapt to full-strength seawater solely through exposure.
- 2) Even if juveniles cannot be directly induced to physiologically adapt to full-strength seawater, they could probably still use it for shorter times in an ecological situation. For example, they could volitionally enter seawater to forage but exit before ion levels in their blood plasma became lethal. Presumably this would take longer in larger juvenile salmonids, and so larger individuals might have greater access to seawater habitats.
- 3) The distinction between ion-importing, isotonic and ion-exporting habitats is not a sharp threshold but rather a gradual transition.
- 4) This rating scheme does not account for the actual process of inducing tolerance (physiological adaptation), which indeed has not really been studied in the wild, where it would occur volitionally rather than as the result of a “seawater challenge.” Perhaps wild juvenile salmonids have behavioral strategies to induce salinity tolerance that differ in important ways from laboratory techniques for doing so.

Based on the above information, the following salinity (‰) rating scheme was developed for freshwater- and marine-acclimated residents (Table 2; Appendix A):

Table 2. Salinity (‰) rating scheme for freshwater- and marine-acclimated residents.

Hypotonic	Isotonic	Hypertonic	Marine
< 10 ‰	10 - 15 ‰	15 - 28 ‰	> 28 ‰

Definitions:

Hypotonic: Fresh water to moderately saline conditions, with low energy cost of ion regulation. Allows high growth potential for both freshwater- and marine-acclimated residents.

Isotonic: Negligible energy cost of ion regulation for both freshwater-acclimated and marine-acclimated residents. Allows for most efficient transfer of food energy to growth.

Hypertonic: Highly saline conditions, but less saline than seawater. For freshwater-acclimated residents, stimulates physiological adaptation to salty water, incurring a high energetic cost in the process. After several weeks these juvenile steelhead become marine-acclimated with a low energy cost of ion regulation and positive to high growth potential.

Marine: Salinity similar to that of the sea. For freshwater-acclimated residents, unsuitable conditions probably causing death with sufficiently long exposure. For marine-acclimated residents, moderately energy demanding that somewhat impairs growth potential.

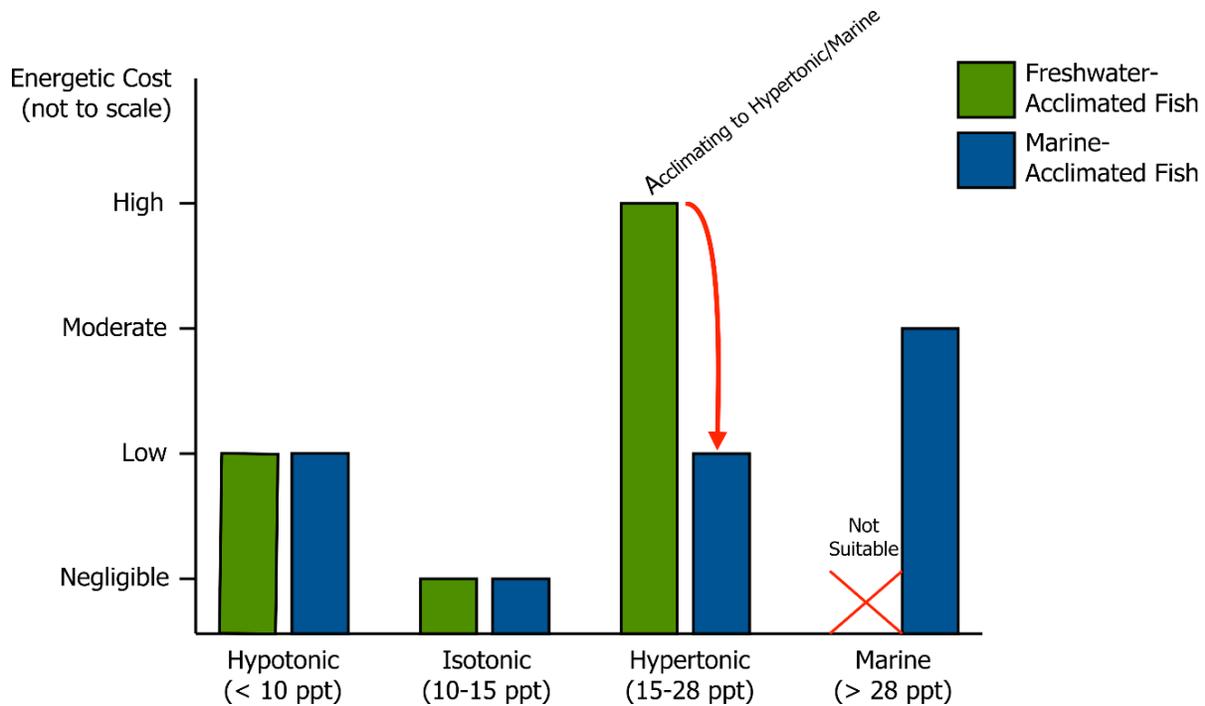


Figure 5. Salinity tolerance and associated energetic demand for freshwater- and marine-acclimated juvenile salmonids.

Dissolved Oxygen and Respiration

Wang et al. (2009) reviewed the physiology of hypoxia in fish, with an emphasis on the effects of hypoxia on growth rate. Although the physiological mechanisms are unclear, the main effect of hypoxia on fish is to reduce their growth rate, primarily by reducing appetite. Hypoxia also reduces the gills' assimilation of oxygen (because of lower oxygen gradients in the gills) and thus limits the maximum metabolic rate that can be maintained, with various effects on the fish. Hypoxia slows down the rate of digestion, although not the overall assimilation of food (it just takes longer). Hypoxia also stimulates a physiological adaptation to lower oxygen levels, increasing the efficiency of the gills over the course of a few weeks. However, this adaptation process does consume energy, as does the digestion of food. The energetic costs of digestion, adaptation, and the lower oxygen assimilation all serve to narrow the aerobic scope of the fish, presumably reducing its ability to respond in behaviorally energetic ways to food and predators.

Saravanan et al. (2013) assessed food intake and oxygen consumption of *O. mykiss* fed to satiation with two diet treatments (balanced vs. imbalanced amino acids) and two oxygen treatments (hypoxia vs. normoxia). They found that *O. mykiss* consumed 29% less food under hypoxia than normoxia and reduced food intake by 11% and 16% respectively when fed the imbalanced diet. However, oxygen consumption per unit body mass was independent of diet under both hypoxia and normoxia. These results supported a hypothesis that food intake in fish is constrained by a set-point value of oxygen consumption.

Robertson et al. (2015) reported that *O. mykiss* exhibit an osmorepiratory compromise common in fishes, in which the branchial modifications that occur to improve O₂ uptake during hypoxia also result in an unfavorable increase in the fluxes of ions and water. This suggests that

physiological adaptation to hypoxia increases the amount of energy required by the gills to actively transport ions across the gill surface to counteract the increased flux. Thus, physiological adaptation to hypoxia is likely to increase the energy cost of maintaining blood plasma ion concentrations for fish not in isotonic water, which includes both fresh water and seawater.

Burt et al. (2013) assessed the impact of moderate intermittent hypoxia (DO of 4 - 5.9 mg/L) on Atlantic salmon growth, food intake, appetite control and innate immunity. Salmon fed under hypoxic conditions ate 25% less food than salmon fed under normoxic conditions, and growth was 24% lower at the end of the experiment. They concluded that leucocyte characteristics suggested a negative impact of hypoxia on leucocyte function independent of feeding level, perhaps compromising the immune system.

Evans (2007) modeled the combined effects of temperature and DO on metabolic scope and power capacity in juvenile lake trout (*Salvelinus namaycush*). Maximum power output for sustained swimming of yearling lake trout occurred at 12 - 20° C and a DO concentration of > 7 mg/L. At 4° - 8° C, temperatures typical of the hypolimnetic summer habitat of juvenile lake trout, maximum power capacity was reduced by 33%, 67%, and 100% at ambient DO concentrations of 7 mg/L, 5 mg/L, and 3 mg/L, respectively. Analysis of power outputs, growth impairment, and recruitment success indicated that attainment of 3/4 power capacity would accommodate most daily life support activities of juvenile lake trout. At 4 - 14° C, the threshold DO concentration for attainment of 3/4 scope-for-activity varied from 7.5 mg/L to 6.6 mg/L, respectively, with a mean and standard deviation of 7.04 ± 0.33 mg/L. A DO criterion of 7 mg/L was recommended for protection of the hypolimnetic habitat of juvenile lake trout.

Behavioral and Ecological Response to Dissolved Oxygen Levels

Svendsen et al. (2012) observed that *O. mykiss* and other fish species make brief excursions from normoxia into areas of severe hypoxia, defined as DO levels below critical oxygen saturation (S_{crit}). S_{crit} is the DO threshold at which standard metabolic rate becomes limited by DO (aerobic scope declines to zero). Tests for *O. mykiss* showed that S_{crit} was 13.5% O₂ saturation. This would probably be temperature dependent since warmer water creates higher metabolic demand for DO. For fish exposed to 10% O₂ saturation for one hour, the peak metabolic rate during recovery was 253 mg O₂ kg⁻¹ h⁻¹ in normoxia (> 95% O₂ saturation) but only half that rate (127 mg O₂ kg⁻¹ h⁻¹) in hypoxic conditions of 30% O₂ saturation. Metabolic recovery lasted nearly twice as long in hypoxia (9.8 h versus 5.2 h). However, the total extra oxygen consumed during recovery did not differ between the two treatments. Thus, slower recovery appears to be the main cost of recovering from severely hypoxic conditions (< S_{crit}) when the recovery is under moderately hypoxic conditions versus normal conditions. Such cost might affect fitness by affecting feeding or predator-avoidance behaviors.

In a whole-lake experiment, Barrow and Peters (2001) installed an aeration system to increase DO and used ultrasonic telemetry to determine movements, habitat use, and distribution of 51 rainbow trout (*O. mykiss*) before and after treatment. *O. mykiss* preferred areas with abundant food items, water less than 5 cm deep, DO > 6 mg/L, and temperatures < 20° C. Sixty-nine percent of all trout locations were in shallow areas where benthic macro-invertebrate densities were significantly higher than in other portions of the lake. Moore et al. (2014) describe a paired-whole-lake experiment on *O. mykiss* and *S. fontinalis*, in which a line diffuser was used to oxygenate the hypolimnion of one of the lakes to increase summer trout habitat. Volume of

suitable habitat increased from a low of 0% pre-oxygenation, to 100% of the hypolimnion following oxygenation. Summer trout movements and habitat utilization were assessed for six years using ultrasonic telemetry, archival tags, gillnetting, and hydroacoustics. Trout utilized the oxygenated hypolimnetic habitat more frequently relative to pre-oxygenation years, and also relative to the other, oxygenated lake. Swim speeds significantly decreased with oxygenation. This seems counterintuitive; since the higher DO concentration should enable greater physical activity. However, the authors note that prior to oxygenation the trout were confined themselves to higher temperature water to escape the hypolimnetic DO deficit, increasing their metabolic rates. This necessitated that fish swim faster and farther in search of low-density zooplankton prey. The authors hypothesized that oxygenation allowed trout to use deeper, formerly anoxic waters with more favorable temperatures and more favorable prey conditions, permitting slower swim speeds and likely reducing stress.

To investigate carrying capacity and growth rates of rainbow trout in a lake, Blair et al. (2013a) used the Wisconsin bioenergetics model and field observations to assess how stocking rate, release timing, and prey abundance affected growth and feeding. Stocking timing had no effect: autumn releases were smaller than spring releases, but grew faster and had similar lengths and weights to spring cohorts after two years. The higher growth of autumn releases may have been due to: (1) temperature is more suitable for growth in autumn-winter than in spring-summer; and, (2) prey for small trout is abundant in autumn. This suggests that moderately productive warm-temperate lake ecosystems are highly suitable for trout growth and survival in winter but less so in summer, when lake stratification and high nutrient levels may create conditions suitable for algal blooms and hypolimnetic deoxygenation.

Blair et al. (2013b) analyzed long-term mark-recapture data on *O. mykiss* in nine closely-located, warm-temperate lakes of contrasting morphometry, stratification and mixing regime, and trophic state. In deep oligotrophic and mesotrophic lakes, trout growth rates increased with increasing indices of lake productivity. In shallow eutrophic lakes where fish habitat volume is constrained by temperature and DO, trout growth rates declined with increasing productivity. Growth rates were higher in lakes with greater volumes of favorable habitat (*i.e.*, DO > 6.0 mg/L and temperature < 21° C) and lower in lakes with increased turbidity, chlorophyll a, and nitrogen concentrations. Their findings suggest that increases in lake productivity and temperatures as a result of global climatic change are likely to be more detrimental to salmonid habitat quality in shallower, productive lakes.

Juvenile Atlantic salmon (*S. salar*) of different age classes exhibit different behavioral responses to elevated temperatures (> 23° C). Yearling (1+) and 2-year-old (2+) juvenile salmon often cease feeding, abandon territorial behavior, and swim continuously in aggregations in cool-water sites; whereas young-of-the-year continue foraging and defending territories. In a laboratory study, Breau et al. (2011) found that oxygen consumption of age 2+ fish increased with temperature and plateaued at 24° C, a temperature at which feeding ceases and lactate levels increase in muscle and blood (indicating anaerobic metabolism). By contrast, oxygen consumption in age 0+ fish did not plateau, feeding continued, and muscle lactate did not increase, even at the highest temperatures tested (28° C). Thus, older (larger) salmon in rising temperatures appear to lose aerobic scope at a lower temperature than younger (smaller salmon), and sacrifice feeding to retreat to thermal refugia sooner than smaller salmon. The likely reason is surface-to-mass scaling relationships that aerobically constrain basal metabolism at lower temperatures in larger salmon.

Plumb et al. (2014) coupled dynamic optimization and bioenergetics models to ask if lake trout (*S. namaycush*) depth distribution is structured by temperature, food availability, and predation risk, so as to maximize the reproductive mass by autumn spawning. The model was compared to data on depths occupied by acoustic-tagged trout and empirical daily thermal-depth profiles from a small boreal shield lake in Ontario. The depths and temperatures occupied by simulated fish most closely resembled those of the tagged fish when a shallow-water risk of predation was included in the model. Annual differences suggest that compared to years with cool surface water, in years with a warm thermal stratification pattern, lake trout show less use of shallow (warm), productive habitats, resulting in fish having markedly less reproductive mass during the year. The reason for staying in cooler deeper water appears to be avoidance of predation risk. The model suggested that in consequence, mass allocated to reproduction may be lower in these stratified years, yet survival may be higher because the fish avoid the warm, productive, yet risky surface waters and stay in cooler deeper conditions.

Plumb and Blanchfield (2009) compared the *in situ* habitat use of acoustic-tagged lake trout (*S. namaycush*) to the habitat volumes of the lake predicted from traditional combinations of temperature and DO boundaries. A widely used criterion of 8 - 12° C underestimated the habitat use of lake trout by 68%-80%. Instead, a criterion combining temperature (< 12° C) and DO (> 6 mg/L) most closely matched the observed habitat use by lake trout, and showed a similar seasonal trend in spatial distribution as the tagged fish.

Based on the above information, the following DO (mg/L) rating scheme was developed for freshwater- and marine-acclimated residents (Table 3; Appendix A):

Table 3. Dissolved oxygen (mg/L) rating scheme for freshwater- and marine-acclimated residents.

Minimal or no impairment	Moderate impairment	Severe impairment	Unsuitable
> 6 mg/L	4 – 6 mg/L	3 – 4 mg/L	< 3 mg/L

Definitions:

Minimal or no impairment: Dissolved oxygen has little to no effect on metabolism and growth potential.

Moderate impairment: Dissolved oxygen has minor impairment on growth potential, but positive growth (weight gain) is achievable depending on temperature, salinity, and food availability.

Severe impairment: Dissolved oxygen forces no or negative growth potential (weight loss) at most temperatures and salinities.

Unsuitable: Dissolved oxygen is severely limiting and cannot sustain metabolic demand under any circumstances, eventually causing death.

Inadequacy of the Water Quality Criteria

In general our scheme of water quality rating criteria should be applied with caution, due to likely complex interactions in how temperature, salinity and DO affect salmonid energetics and foraging behaviors stemming from those energetics. For example, because metabolic rate increases with water temperature, it is likely that some levels of DO that are sufficient to prevent impairment at low temperatures may not prevent impairment at high temperatures. Similarly, the energetic demand of physiologically adapting to high salinity may interfere with tolerance for high water temperatures, which also has high energetic demand. Thus, our categorical scheme does not fully capture the competing demands for unacclimated juveniles to forage in cool, food-abundant marine layers but retreat to warm fresh water layers when blood plasma ion concentrations reach dangerous levels. Understanding these sorts of interaction effects requires quantitative bioenergetic and foraging models, but developing and applying such models is beyond the scope of this report. We expect that the application of our categorical rating scheme to outputs of the QCM will likely suggest whether such development of quantitative models is warranted, and guide which sorts of interaction effects are most important to explicitly model.

Prey Availability in the Russian River Estuary and other California Estuaries

Excepting most insect larvae (which predominantly occupy benthic habitats or on submerged vegetation until they emerge as adults) and gastropods snails, all the amphipods, isopods, mysids and corixid beetles that form the dominant prey of juvenile steelhead display epibenthic behavior. The epibenthic macroinvertebrates live on top of or closely associated with the bottom substrate but can be found moving over it. The one variant on this generalization is that the Corophidae amphipods (e.g., *Americorophium* spp.) live in tubes in the surface of sand-mud bottom substrate (e.g., Miller 1984) and (predominantly the males) move out of the tubes to appear in the epibenthos. Estuarine epibenthic crustaceans such as *E. confervicolus* are known to a wide variety of substrates but have been characterized as having some habitat fidelity despite their dispersion capabilities (Pomeroy and Levings 1980; Stanhope and Levings 1985; Stanhope *et al.* 1992).

The prey observed in the diet of steelhead in the Russian River Estuary are primarily available to fish feeding in intertidal and shallow subtidal habitats. SCWA-UW studies of prey availability primarily use three methods to sample these potential foraging habitats: (1) benthic cores; (2) an epibenthic net; and, (3) an epibenthic (channel) sled (Seghesio 2011; Simenstad *et al. in review*). The epibenthic net (“net to shore”) samples the water’s edge within 10m of the shore and the epibenthic sled samples in the thalweg and shelf portions of the estuary channel. In earlier sampling (Seghesio 2011), insect fallout traps were also utilized to sample insects falling to the surface at the waters’ edge, but these have not been deployed in recent years. We also monitor the vertical water column for zooplankton, but no planktonic prey have been found in the juvenile steelhead diet.

Generally, the highest densities of these prey were found in the benthic core samples, on the order of 1,000 - 50,000 organisms/m² for individual prey taxa (e.g., Simenstad *et al. in review*). Much of these high densities may be attributed to high densities of *Ameriocrorophium* spp. in their tubiculous colonies. In comparison, densities of these prey taxa in the epibenthic net from shallow waters along the estuary shoreline averaged an order of magnitude less, seldom over 1,000 organisms/m², except for the gastropod snails, which were estimated to average

~5,000 organisms/m² on some occasions. The epibenthic channel sled typically accounted for similar or relatively half the densities of the epibenthic net along the shoreline, commonly 200 - 600 organism/m² when most abundant. It should be noted that the sampling efficiencies of the two epibenthic net samplers is thought to be considerably less than the benthic core sampler because the net is constrained to pass over substrate, algae and other plants, where most of these epibenthic prey are nestled. However, we have personally observed dense concentrations of amphipods, isopods and corixids moving in with increasing water levels, and high (“cloud”) concentrations of *N. mercedis* mysids, nestled in pockets along the bottom, suggesting behavioral affiliations with the substrate of intertidal/shallow subtidal habitat. As mentioned previously, basically no prominent prey of steelhead are captured in the insect fallout trap or the zooplankton sampling. Furthermore, we found densities of prey organisms to be higher early in the sampling period and diminish by roughly an order of magnitude by late summer. Compared to open-estuary conditions, during closed inlet conditions there is a relatively minor gradient of prey density distribution increasing from their deeper channel to shallower marginal habitats. Shortly after a closure, there appears to be a redistribution of prey into the increased shallow water habitat.

These prey are commonly found at high densities in the shallow intertidal and shallow subtidal zones of northeastern Pacific estuaries (Needham 1940, Shapovalov and Taft 1954, Meyer et al. 1981, Robinson 1993, Seghesio 2011, Daly et al. 2014). Studying the benthic and epibenthic distribution of macroinvertebrates in Pescadero Lagoon, California, Robinson (1993) found prey abundance was low in the deep-water when DO levels were also low. They found *Chironomus* sp. in fresh shallow-water primarily during closed conditions and almost never during open conditions. When the estuary was open, *N. mercedis* was found to be abundant at all depths but more abundant in the shallow habitat when the estuary was closed. Although *G. insulare* were found to be more abundant deeper during open conditions, abundance during closed conditions increased in the shallower stations and sharply decreased at the deep stations. When the estuary was open, *Americorophium* spp. densities were highest at the stations not exposed during low tides and demonstrated a rapid colonization after a pesticide kill. Interestingly, these tubicolous amphipods have been found above the normal water line in moderate density (3500 organisms/m²), suggesting an adaptation to fluctuating lagoon levels (Needham 1940).

In their studies of differential growth of steelhead in riverine and estuarine reaches of Scott Creek, central California, Hayes et al. (2008) described similarly large numbers of *Eogammarus* spp., *Corophium* spp., *Neomysis* spp. and *Gnorimosphaeroma* spp. associated with algae in the Scott Creek Estuary during its closed phase.

Diet Composition in the Russian River Estuary and other California Estuaries

The analysis of 509 juvenile steelhead diets in the Russian River Estuary (2009 - 2015) has demonstrated extremely consistent prey spectra that are focused on a limited number of primarily epibenthic crustaceans (with only a few exceptions). Based on all metrics of dietary composition (frequency of occurrence, numerical and gravimetric composition), the predominant prey are the gammarid amphipods *Eogammarus confervicolus*, *Americorophium salmonis*, *A. spinicorne*, and the isopod *Gnorimosphaeroma insulare* (Seghesio 2011, Simenstad et al., *in review*). Corixid beetles (water boatman) and chironomid insects (adult, larva and pupa), the mysid *Neomysis mercedis* and nereid polychaetes and gastropod snails (tentatively identified as the New Zealand mud snail, *Potamopyrgus jenkinsi*) constitute prey of relative secondary importance. Incidental

prey were almost exclusively insects. Although, the predominant prey consisted of lower energy taxa, some of the secondary and incidental prey, especially corixid beetles, mysids and insects, have higher energy densities that can provide bioenergetic benefits (Seghesio 2011).

Overall, diversity of prey consumed tends to be higher early in the May to December sampling period, declining as summer moves into fall. Spatial differences in diet include increased occurrence of insects and corixid beetles in the upper reach and greater occurrence of mysids in the lower reach. During closed conditions, juvenile steelhead consumed gastropods and adult chironomids more often and mysids less often.

Published literature and other documentation of juvenile steelhead diet composition reflects similar diet composition, especially in comparable estuarine settings as the Russian River Estuary. In 1933, the diet composition of yearling juvenile steelhead in Waddell Creek Lagoon consisted of over 93% *E. confervicolus* (Needham 1940). Similar foraging behaviors were observed during the mid-1980's in the Pescadero Lagoon (Martin 1995). In addition to *E. confervicolus*, Martin (1995) found *Americorophium* spp., *G. insulare*, *Chironomus* sp., and *N. mercedis* commonly consumed by rearing juvenile steelhead. Furthermore, the stomach contents of Redwood Creek Lagoon salmon and trout (Chinook, coho, cutthroat, and steelhead) were dominated by amphipods (45%) and rarely consisted of prey items with a terrestrial origin (1.2%) (Ward and Sepulveda 2014).

Studies of the Mattole River Estuary and Lagoon by Zedonis (1992) characterized the diets of juvenile steelhead after lagoon formation as exhibiting “a benthic feeding strategy” where the dominant prey were identified as the epibenthic *Corophium* amphipods and isopods and aquatic insects (dipterans, tricopteran and ephemeropteran larvae). Prey dominance varied by region in the lagoon, where *Corophium* spp. dominated in the lower lagoon and tricopteran larvae in the upper lagoon.

Conceptual Habitat Zones: Foraging Habitat and Predation Risk

Limited information exists relative to the confounding factors associated with predation risk (or avoidance) and foraging behavior of riverine or estuarine rearing salmonids. However, it is commonly inferred in aquatic ecology that individual fish (*i.e.*, salmonids) are often confronted with weighing the gross benefits of exploiting high growth potential areas and feeding opportunities with the risk of being susceptible to avian and/or other aquatic predation. Dill and Fraser (1984) showed that juvenile coho exhibit less risky feeding behavior in the presence of predators, but when they were hungry they exhibited riskier feeding behavior in the presence of predators. Other evidence from the literature supports a balance between light penetration great enough to allow successful (visual) foraging but poor enough to reduce or minimize predation risk from visual predators. Harvey and Nakamoto (2013) suggested that multiple mechanisms linked predation risk to population dynamics, and therefore argued for additional effort to identify patterns of spatiotemporal variation in predation risk.

In the Russian River Estuary, unpublished data⁴ show growth rates as high or higher than what has been reported in the literature for wild juvenile steelhead (Hayes et al. 2008). The subsurface (epibenthic) foraging habitat appears to provide very good opportunity for growth. Similarly, Fuller (2011) found that acoustically tagged and untagged juvenile steelhead within the estuary

⁴ Unpublished data from Sonoma County Water Agency and University of Washington, Wetland Ecosystem Team.

also showed accelerated growth. Matsubu et al. (2016 *submitted*) found that acoustically tagged juvenile steelhead in the Russian River Estuary occupied a mean depth of 1.4 m ([open inlet = 1.4 m, closed inlet = 1.3 m], SD = 0.8 m; n = 25,663 detections from 67 individuals) with no differences in depth among reaches. Although the mechanisms are unknown, deeper habitats (> 5 m) with lower DO concentrations (< 4 mg/L) were not occupied. Additionally, Fuller (2011) detected acoustically tagged juvenile steelhead most often in habitat shallower than three meters and also observed foraging behavior along the littoral zone (< 1 m). Quiñones and Mulligan (2005) conducted snorkel surveys to determine the habitat use of juvenile salmonids in the Smith River Estuary, California. They found juvenile trout and steelhead (*O. clarkii clarkii* and *O. mykiss*) most often in the littoral zone of the estuary.

The extent to which predation may be occurring and therefore impacting survival is unknown in the estuary; however, the literature suggests that in cases where food is abundant and readily accessible, individuals are unlikely to be exhibiting risky foraging behavior (Dill 1983, Dill and Fraser 1984). Whether or not foraging opportunity has a greater influence on depth preferences than predator avoidance, we must recognize how predation risk may influence habitat use and the potential consequences of that risk on the populations.

The aforementioned review suggests that there are five foraging habitats (Figures 6 and 7) with four associated predation risk depths (Table 4) that make up conceptual habitat zones (Table 4) for the estuary. Moreover, these conceptual habitat zones are based on observed habitats occupied, foraging behavior, and productivity/prey availability: Shallow/shoal littoral (< 1 m total depth), high prey availability; surface limnetic (top 1 m where total depth > 1 m), low prey availability; subsurface epibenthic (total depth 1 - 5 m), high prey availability; subsurface limnetic (from 1 – 5 m where total depth > 5 m), low prey availability; and profundal (> 5 m to bottom), low prey availability. We emphasize however that these zones are conceptual models at this point, based on literature review rather than on predation data from the Russian River Estuary itself.

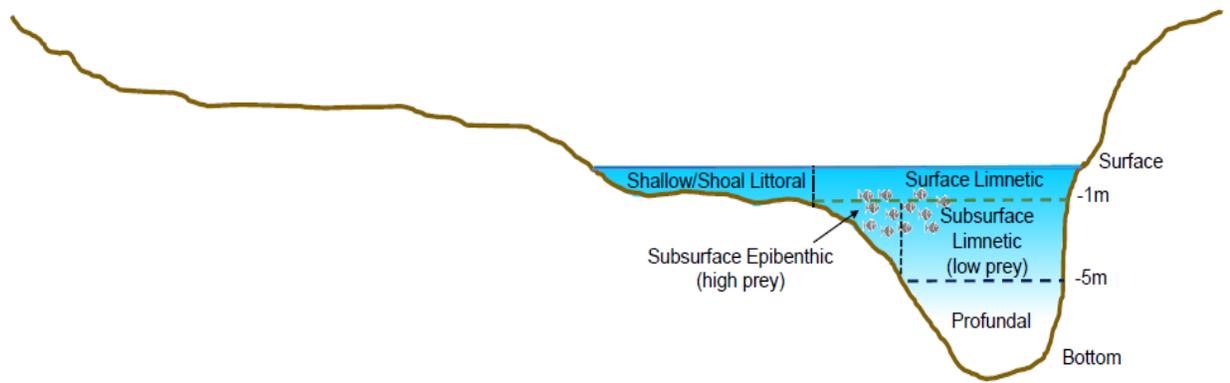


Figure 6. Foraging Zones open conditions for the Russian River Estuary, CA.

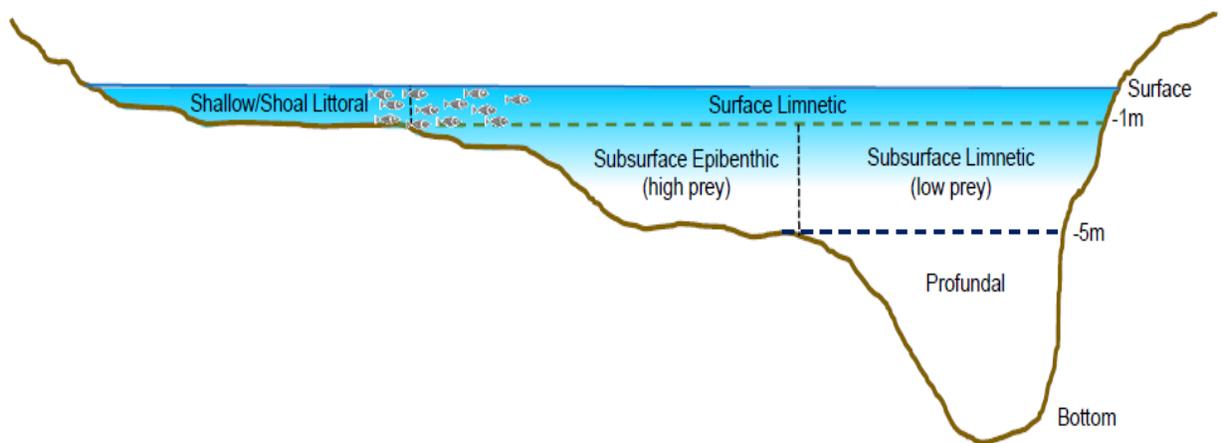


Figure 7. Foraging Zones closed/perched conditions for the Russian River Estuary, CA.

Table 4. Conceptual habitat zones for freshwater- and marine-acclimated residents.

Zone Depth	Total Depth	Habitat Conceptual Zone	Foraging Habitat	Predation Risk
0 – 1 m	< 1 m	Shallow/Shoal Littoral	Sunlight penetrates to bottom (high prey availability)	Shallow water risk: high avian predation risk, low aquatic predation risk
0 – 1 m	> 1 m	Surface Limnetic	Within depths of sunlight penetration (low prey availability)	Surface water risk: high avian predation risk, high aquatic predation risk
1 – 5 m	> 1 m and ≤ 5 m	Subsurface Epibenthic	Below surface foraging zone; within depths of sunlight penetration (high prey availability)	Subsurface open water risk: low avian predation risk, moderate aquatic predation risk
1 – 5 m	≥ 5 m	Subsurface Limnetic	Below surface foraging zone; within depths of sunlight penetration (low prey availability)	
5 m to bottom	≥ 5 m	Profundal (Stagnant)	Little or no light penetration and poor circulation (low prey availability or unsuitable due to hypoxia/anoxia and low light levels)	Unoccupied/no predation risk

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Appendix A

NOAA's Habitat Blueprint ~ Russian River Habitat Focus Area

Project: Russian River Water Quality Modeling to Inform Time-Dependent Availability of Estuarine Habitat for Salmonids

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Task: Develop a rating scheme for juvenile salmonids for evaluating output from the spatially-explicit Russian River Estuary Quantitative Conceptual Model (QCM; temperature, DO, salinity, depth). This initial criteria targets summer rearing juvenile salmonid productivity and growth associated with the identified water quality parameters.

Life Stage Categories: Two juvenile steelhead categories and their water quality tolerances have been selected to inform the water quality habitat and productivity components within the estuary during the dry season (generally spring through fall). We considered both categories as encompassing juvenile steelhead that rear in the estuary. Therefore, we did not focus on smolts¹ because they theoretically do not rear in the estuary, but instead spend a relatively brief period migrating through the estuary during a time (majority before June) when water quality conditions are generally suitable for salmonids that can tolerate full strength seawater.

1. **Freshwater-acclimated Residents:** Individuals that rear in the estuary prior to smoltification, but are limited in their capacity to osmoregulate in seawater. These individuals may increase their capacity to excrete salt ions over time and therefore become fully marine-acclimated residents.
2. **Marine-acclimated Residents:** Individuals that rear in the estuary prior to smoltification and have the capacity to osmoregulate in full strength seawater (> 28 ‰).

Water Quality Parameters: The water quality parameters used to inform habitat availability and productivity components for juvenile salmonids in the estuary include temperature (° C), Dissolved Oxygen or DO (mg/L), and salinity (‰). Suboptimal levels of these water-quality parameters involve increased energy expenditure, slower growth, and eventually mortality at higher levels, as summarized in the categorical rating scheme. They also involve complex interactions, such as higher oxygen demand at higher water temperatures or salinities, which cannot be fully captured by this categorical scheme. Therefore, we have provided a write-up that discusses our rationale for each rating scheme, the complexities of salmonid physiology and bioenergetics, and the subsequent limitations of the modeling outputs and recommendations to address them (*e.g.*, bioenergetics models, partial life history model, *etc.*).

Water depth (m) is an output of the QCM and will be used to evaluate juvenile salmonid foraging opportunities and prey availability, which tend to be structured by water depth and characteristics of the benthic substrate. Water depth considerations also include tradeoffs between foraging opportunities (location of prey availability) both vertically in the water column and horizontally across the width of the estuary in relation to avian and aquatic predation risk.

¹ We define the term smolt as juvenile salmonids that have gone through the parr-smolt transformation (*i.e.*, smoltification) via a suite of behavioral, morphological, and physiological changes as they migrate directly to sea for the first time (McCormick 2013). This downstream seaward migration generally occurs before June in the Russian River.

1. Temperature (° C) rating scheme: Freshwater- and marine-acclimated residents

Fastest growth	Positive growth	No or Negative growth	Unsuitable
14° - 18° C	< 14° or 18° - 21° C	21°- 25° C	> 25° C

Fastest growth: Temperature allows for the most rapid growth when food availability is unlimited.

Positive growth: Temperature allows for positive growth (weight gain) under most levels of DO, salinity, and food availability.

No or negative growth: Usually produces high metabolic demand and negative growth (weight loss) even when food is available.

Unsuitable: Highly stressful and generally cannot sustain metabolic demand for more than a day without death or injury.

2. Dissolved Oxygen (mg/L) rating scheme: Freshwater- and marine-acclimated residents

Minimal or no impairment	Moderate impairment	Severe impairment	Unsuitable
> 6 mg/L	4 – 6 mg/L	3 – 4 mg/L	< 3 mg/L

Minimal or no impairment: Dissolved oxygen (DO) has little to no effect on metabolism and growth potential.

Moderate impairment: DO has minor impairment on growth potential, but positive growth (weight gain) is achievable depending on temperature, salinity, and food availability.

Severe impairment: DO forces no or negative growth potential (weight loss) at most temperatures and salinities.

Unsuitable: DO is severely limiting and cannot sustain metabolic demand under any circumstances, eventually causing death.

3. Salinity (‰) rating scheme: Freshwater- and marine-acclimated residents

Hypotonic	Isotonic	Hypertonic	Marine
< 10 ‰	10 - 15 ‰	15 - 28 ‰	> 28 ‰

Hypotonic: Fresh water to moderately saline conditions, with low energy cost of ion regulation. Allows high growth potential for both freshwater- and marine-acclimated residents.

Isotonic: Negligible energy cost of ion regulation for both freshwater-acclimated and marine-acclimated residents. Allows for most efficient transfer of food energy to growth.

Hypertonic: Highly saline conditions, but less saline than seawater. For freshwater-acclimated residents, stimulates physiological adaptation to salty water, incurring a high energetic cost in the process. After several weeks these juvenile steelhead become marine-acclimated with a low energy cost of ion regulation and positive to high growth potential.

Marine: Salinity similar to that of the sea. For freshwater-acclimated residents, unsuitable conditions probably causing death with sufficiently long exposure. For marine-acclimated residents, moderately energy demanding that somewhat impairs growth potential.

4. Conceptual Habitat Zones: Freshwater- and marine-acclimated residents

Zone Depth	Total Depth	Habitat Conceptual Zone	Foraging Habitat	Predation Risk
0 – 1 m	< 1 m	Shallow/Shoal Littoral	Sunlight penetrates to bottom (high prey availability)	Shallow water risk: high avian predation risk, low aquatic predation risk
0 – 1 m	> 1 m	Surface Limnetic	Within depths of sunlight penetration (low prey availability)	Surface water risk: high avian predation risk, high aquatic predation risk
1 – 5 m	> 1 m and ≤ 5 m	Subsurface Epibenthic	Below surface foraging zone; within depths of sunlight penetration (high prey availability)	Subsurface open water risk: low avian predation risk, moderate aquatic predation risk
1 – 5 m	≥ 5 m	Subsurface Limnetic	Below surface foraging zone; within depths of sunlight penetration (low prey availability)	
5 m to bottom	≥ 5 m	Profundal (Stagnant)	Little or no light penetration and poor circulation (low prey availability or unsuitable due to hypoxia/anoxia and low light levels)	Unoccupied/no predation risk

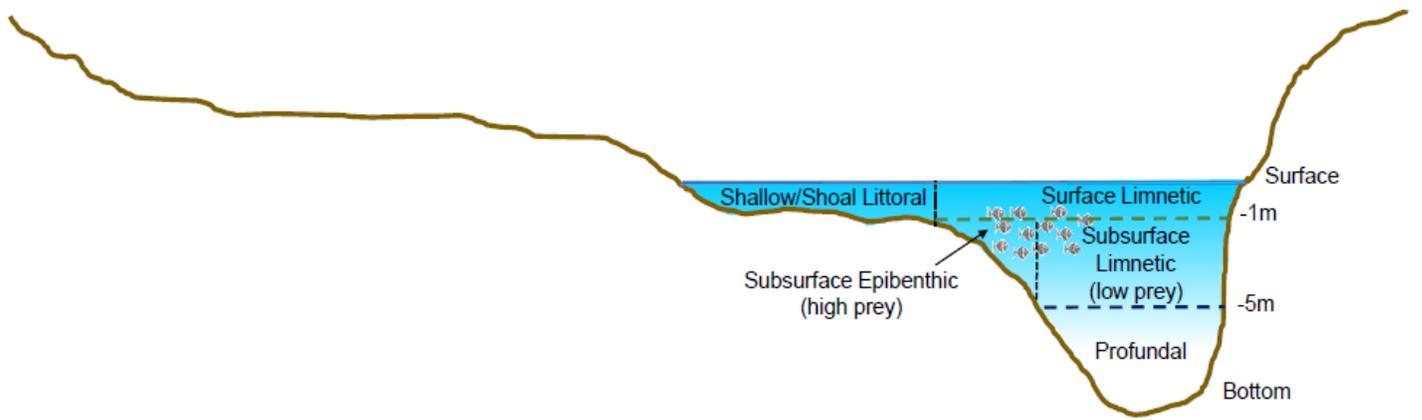


Figure 1. Foraging Zones open conditions for the Russian River Estuary, CA.

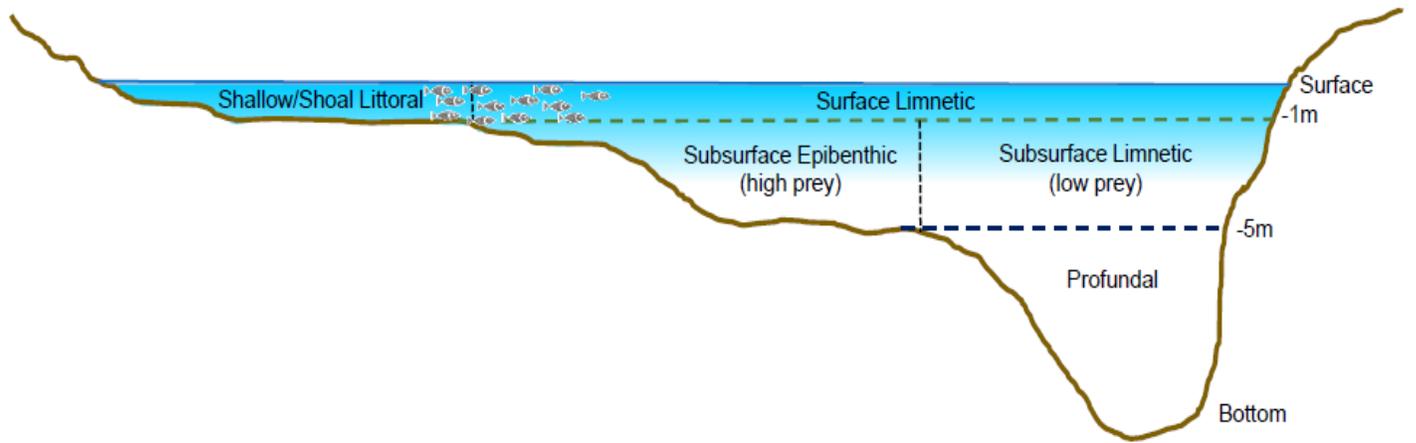


Figure 2. Foraging Zones closed/perched conditions for the Russian River Estuary, CA.