Public Comment
303(d) List of 2014 & 2016 CA Integrated Report
Deadline: 7/10/17 by 12 noon

WISHTOYO
CHUMASH FOUNDATION

VENTURA COASTKEEPER

RECEIVED
7-10-17
SWRCB Clerk

July 10, 2017

Chair Felicia Marcus and Board Members
c/o Jeanine Townsend, Clerk to the Board
State Water Resources Control Board
1001 I Street, 24th Floor
Sacramento, CA 95814
commentletters@waterboards.ca.gov

Comment #4

VIA ELECTRONIC MAIL: WQAssessment@waterboards.ca.gov;
commentletters@waterboards.ca.gov

Re: Comment Letter - 303(d) List Portion of the 2014 and 2016 California Integrated Report

Dear Chair Marcus and California State Water Resources Control Board ("Board") Members:

On behalf of Wishtoyo Foundation and our Ventura Coastkeeper Program, please accept the following comments on the 303(d) List portion of the 2014 and 2016 California Integrated Report ("Integrated Report" or "303(d) List")

4.01 In reviewing the 303(d) List, it has come to our attention that almost all of the proposed 303(d) listings (See Attachment A) and accompanying supporting data timely submitted on August 30, 2010 by Wishtoyo Foundation's Ventura Coastkeeper Program ("VCK") were not assessed for inclusion in the 303(d) List[1].

4.02 We thus respectfully request the Board assess all of VCK's proposed 303(d) Listings and accompanying data submitted in 2010, and ensure VCK's proposed listings are included in the 303(d) List. All of VCK's proposed listings meet the requirements for listing in the State Water Resources Control Board's Water Quality Control Policy for Developing California's Clean Water Act Section 303(d) List. Notably, as demonstrated by VCK August 30, 2010 proposed listing submission, VCK's watershed monitoring data supporting the proposed listings were collected and analyzed in accordance with VCK's Quality Assurance Project Plan (QAPP) approved by the Los Angeles Regional Water Quality Control Board.

---

[1] See Attachment B for Los Angeles Regional Board staff worksheet detailing some of the VCK proposed listings and accompanying data improperly not assessed to date for the Draft 2016 303(d)/305(b) List.

4.03

Furthermore, we ask the Board to include on the list, the dissolved oxygen ("DO") data submitted by VCK that supports the Santa Clara River Estuary ("Estuary") being included on the 303(d) List for DO impairment. Even one event where DO levels drops below Basin Plan thresholds can be catastrophic for native and endangered aquatic life, including the Southern California Steelhead[2] and Tidewater Goby that use the Estuary as habitat and that need healthy and suitable water quality in the Estuary to survive and recover. It only takes one event of low DO for these species to perish, and the Board and Los Angeles Regional Board was provided over 200 separate data entries indicating that DO fell in the Estuary below Basin Plan thresholds and non-harmful levels for aquatic life. Attached to this letter is are two studies by a Regional Board Scientist (Carter 2005 and 2008) that further details the harms of low DO on aquatic life and native and endangered species, including Southern California Steelhead.

VCK's mission is to protect, preserve, and restore the ecological integrity and water quality of Ventura County's inland and coastal waterways. In 2009 and 2010, VCK, in coordination with the Los Angeles Regional Water Quality Control Board and State Water Resources Control Board Clean Water Team, dedicated a tremendous amount of resources to its watershed monitoring program that resulted in VCK's proposed 303(d) Listings. These resources include VCK running volunteer stream teams, utilizing staff time to collect and analyze water quality data, purchasing and maintaining field equipment, and running a laboratory. It would be a shame, and detrimental to Ventura County's inland and coastal waterways and their beneficial uses, if the water quality impairments discovered, rigorously documented by VCK, and provided to the state did not result in 2016 303(d) Listings, especially on the account that they were not assessed. It is without second thought that the Los Angeles Regional Board assessing our proposed 303(d) Listings and accompanying data from August 30, 2010, and ensuring these proposed listings are included in the 2016 303(d) List, is critical to the protection of Ventura County's waters for all the people, wildlife, communities, and the Chumash Native American Peoples that depend upon clean and healthy waters to sustain their health, wellbeing, and life ways. 4.04

4.05

In addition, we note that based on VCK's submitted watershed monitoring program data indicates that on 5 out of 7 VCK monitoring events on Nicholas Canyon Creek (San Nicolas Canyon Creek) downstream of PCH, the presence of trash pollution exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL, that San Nicolas Canyon Creek should be included on the 303(d) List for trash. The Board Staff report is in error that there were only 4 out of 6 monitoring events where this trash exceedance was demonstrated. Of note, the Chumash People use this creek (and

---

[2] Juvenile Southern California Steelhead utilize estuaries as over-summering and rearing habitat for extended periods of time. (See attached Hayes, et. al (2008); See attached Bond (2006).) The National Marine Fisheries Service ("NMFS") has designated the Estuary as critical habitat under the federal Endangered Species Act, and the NMFS Steelhead Recovery Plan (January 2012) prioritizes Santa Clara River Estuary habitat restoration and protection as a critical action for the survival and recovery of the species. For NMFS Steelhead Recovery Plan visit: http://www.westcoast.fisheries.noaa.gov/protected_species/salmon_steelhead/recovery_planning_and_implementation/south_central_southern_california_coast/south_central_southern_california_coast_recovery_publications.html (last visited March 24, 2017).

specifically the sampled segment) for cultural practices and ceremonial use. There is Chumash ceremonial REC-1 water contact uses and non water contact uses here. In addition, the QAQC and minimum number of exceedances was met, which further requires the 303(d) Listing for trash.

Thank you for considering our comments. Please feel free to contact me with any questions.

Sincerely,

Jason Weiner
General Counsel, Water Initiative Director
Wishtoyo Foundation and its Ventura Coastkeeper Program
jweiner.venturacoastkeeper@wishtoyo.org
(805) 823-3301

VENTURA COASTKEEPER®
3875-A Telegraph Road #423, Ventura, California 93003
Phone (805) 658-1120 • Fax (805) 258-5135 • www.wishtoyo.org

August 30, 2010

Jeffrey Shu, State Water Resources Control Board
Division of Water Quality
P.O. Box 100
Sacramento, CA 95812-0100
VIA ELECTRONIC MAIL: jshu@waterboards.ca.gov

RE: **Region 4, Notice of Public Solicitation of Water Quality Data and Information for 2012 California Integrated Report [Clean Water Act Sections 305(b) and 303(d)]**

Dear Mr. Shu:

Wishtoyo Foundation's Ventura Coastkeeper Program (VCK), which represents over 700 Ventura County residents, appreciates the opportunity to submit water quality data and information for the 2012 California Integrated Report for Los Angeles Region 4 pursuant to Clean Water Act Sections 305(b) and 303(d).

VCK's Watershed Monitoring Program has conducted water quality monitoring throughout the Santa Clara River, Ormond Beach, Calleguas Creek, and Nicholas Canyon Creek watersheds from June 2009 to August 2010. After reviewing VCK's monitoring data collected and analyzed in accordance with VCK's Quality Assurance Project Plan (QAPP) approved by the Los Angeles Regional Water Quality Control Board, and after analyzing additional water quality parameters collected by local and state agencies, VCK requests that the following waterbodies[1] are incorporated into the 2012 California Integrated Report for the Los Angeles Region (Region 4) and added to the 2012 Clean Water Act 303(d) impaired waterbody list (List of Water Quality Limited Sections) for the following impairments:

4.06

1.) Nicholas Canyon Creek

---

[1] The locations and description of all waterbodies are included in the attached Wishtoyo Foundation's Ventura Coastkeeper Program's Watershed Monitoring Data Spreadsheet unless otherwise noted. VCK's watershed monitoring locations are part of VCK's watershed monitoring routes, and were chosen based on varying upstream land uses, accessibility, and the need for baseline and real time data to assess the water quality and ecological integrity of Ventura County's inland and coastal waterbodies, and to help pinpoint water quality impairments.

a. **Trash[2]:** VCK's attached watershed monitoring program data indicates that on 5 out of 7 VCK monitoring events on Nicholas Canyon Creek downstream of PCH, the presence of trash pollution exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL.

4.07

2.) San Jon Barranca / Creek

a. **Trash:** VCK's attached watershed monitoring program data indicates that on 8 out of 8 VCK monitoring events on San Jon Barranca downstream of Harbor Boulevard , the presence of trash pollution in San Jon Barranca exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL.

4.08

b. **E. Coli**: VCK's attached watershed monitoring program data indicates that on 5 out of 8 VCK monitoring events on San Jon Barranca downstream of Harbor Boulevard, the presence of E. Coli exceeded the Water Quality Control Plan for the Los Angeles Region ("Basin Plan") single sample numeric water quality standard for E. Coli density of 235/100ml for Fresh Waters Designated for Water Contact Recreation (REC-1).

Pictured below, a child plays in the trash lined San Jon Barranca in the presence of E. Coli pollution.

---

[2] For monitoring of trash at all of VCK's watershed monitoring locations, if the length of the reach monitored for trash is not listed, trash was counted at the sampling location only.

3.) Ormond Beach Lagoon[3]

4.09 a. **Trash:** VCK's attached watershed monitoring program data indicates that on 9 out of 9 VCK monitoring events in the Ormond Beach Lagoon, the presence of trash pollution in the Ormond Beach Wetlands Lagoon exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL.

4.10 b. **E. Coli**: VCK's attached watershed monitoring program data indicates that on 6 out of 32 VCK monitoring events on the Ormond Beach Lagoon, the presence of E. Coli exceeded the Basin Plan single sample numeric water quality standard for E. Coli density of 235/100ml for Fresh Waters Designated for Water Contact Recreation (REC-1).

4.11 c. **pH:** VCK's attached watershed monitoring program data indicates that on 6 out of 8 VCK monitoring events in the Ormond Beach Wetlands Lagoon, pH levels in the Ormond Beach Wetlands Lagoon water column exceeded the Basin Plan single sample numeric water quality standard of 8.5 for Fresh Waters Designated for Water Contact Recreation (REC-1).

4.12 d. **Nitrate:** VCK's attached watershed monitoring program data indicates that on 11 out of 14 VCK monitoring events in the Ormond Beach Lagoon, the concentration of Nitrate in the Ormond Beach Wetland Lagoon water column exceeded the numeric targets for Nitrate at 1 mg/l as derived in the Los Angeles Regional Water Quality Control Board's Machado Lake TMDL[4] and the Nutrient TMDL for Malibu Creek, adopted by USEPA in 2003[5]. In addition, it should be noted that the USEPA guidance value for CWA section 304(a) nutrient criteria specific to the Los Angeles Region (Ecoregion III) is 0.38 mg/l total nitrogen and 0.022 mg/l total phosphorus for protection of aquatic life and recreation.[6]

---

[3] Samping Locations OB-1, OB-5, OB-3(b), OB-4(b) are all 200 meters apart from one another.

[4] Resolution NO. R08-006, Amendment to the Water Quality Control Plan for the Los Angeles Region to Incorporate a Total Maximum Daily Load for Eutrophic, Algea, Ammonia, and Odors (Nutrient) for Machado Lake, California Regional Water Quality Control Board, Los Angeles Region. The Regional Board appropriately included a numeric target for total phosphorus of .1mg/l that was based of the EPA Nutrient Criteria Technical Guidance Manual Lakes and Reservoirs (2000), which does not recommend setting a numeric target for total phosphorus greater than 0.1 mg/L. Additionally, to maintain a balance of nutrients for biomass growth and prevent limitation by one nutrient or another, a ratio of total nitrogen to total phosphorus of 10 is used to derive the total nitrogen numeric target of 1.0 mg/L as a monthly average concentration (Thomann, Mueller, 1987)." (Regional Board Staff Report for Machado Lake TMDL at 35.)

[5] The Nutrient TMDL for Malibu Creek, adopted by USEPA in 2003, provides summer season water quality objectives of 1.0 mg/l total nitrogen and 0.1 mg/l total phosphorous. Other established nitrogen criteria for protection of aquatic life are significantly lower.

[6] See: USEPA, *Ambient Water Quality Criteria Recommendations: Rivers and Streams in Nutrient Ecoregion III* (2000) (EPA 822-B-00-016).

4.13 While, the Basin Plan’s water quality objective for nitrogen is that “Waters shall not exceed 10 mg/l nitrogen as nitrate-nitrogen plus nitrite-nitrogen, 45 mg/l as nitrate, 10 mg/l as nitrate-nitrogen, or 1 mg/l as nitrite-nitrogen or as otherwise designated in Table 3-8,” during the promulgation of the Machado Lake TMDL, the Regional Board determined that the Basin Plan’s water quality objective for nitrogen as applied to aquatic life:

> “is not supportive of the narrative biostimulatory substance water quality objective. The nitrogen objective (10 mg/L) in the Basin Plan is based on criteria acceptable for drinking water and not appropriate to address eutrophic conditions in the lake. A review of available data and scientific literature demonstrates that the numeric objective of 10 mg/L for nitrogen is not sufficiently protective for controlling excessive algal/macrophyte growth and the symptoms of eutrophication in the lake. Therefore, the numeric target for total nitrogen will be more stringent than the existing numeric nitrogen objective in the Basin Plan to ensure attainment of the narrative biostimulatory substances water quality objective. The TMDL and its numeric targets must be developed to ensure protection of all the beneficial uses and attainment of nutrient related water quality objectives specified in the Basin Plan.”[7]

4.14 The Regional Board Staff, in its 2008 update of the Los Angeles Regional Integrated Report for Clean Water Act Section 305(b) Report and Section 303(d) List of Impaired Waters, verified its determinations in their comment for the Machado Lake TMDL by stating:

> “The Basin Plan contains a specific nitrogen (nitrate nitrite) water quality objective, which is established at 10 mg/L nitrogen as nitrate-nitrogen plus nitrite-nitrogen. This objective is specifically set to protect drinking water beneficial uses and is consistent with the California Department Public Health nitrate drinking water standard. This nitrogen water quality objective does not protect waterbodies from impairments related to biostimulatory substances and eutrophication.”

4.) Bubbling Springs

4.15 a. **Trash:** VCK’s attached watershed monitoring program data indicates that on 9 out of 9 VCK monitoring events at Bubbling Springs, the presence of trash pollution in Bubbling Springs exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL

---

[7] Regional Board Staff Report for Machado Lake TMDL at 32, emphasis added.

4.16 b. **<u>E. Coli</u>**: VCK's attached watershed monitoring program data indicates that on 5 out of 11 VCK monitoring events at Bubbling Springs, the presence of E. Coli exceeded the Basin Plan single sample numeric water quality standard for E. Coli density of 235/100ml for Fresh Waters Designated for Water Contact Recreation (REC-1).

5.) J-Street Drain[8]

4.17 **a. <u>Trash:</u>** VCK's attached watershed monitoring program data indicates that on 9 out of 9 VCK monitoring events at J St. Drain, the presence of trash pollution in the J. Street Drain exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL.

6.) Oxnard Industrial Drain (OID)[9]

4.18 **a. <u>Trash:</u>** VCK's attached watershed monitoring program data indicates that on 8 out of 8 VCK monitoring events at the OID, the presence of trash pollution in the OID exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL.

4.19 b. **<u>E. Coli</u>**: VCK's attached watershed monitoring program data indicates that on 5 out of 11 VCK monitoring events at the OID, the presence of E. Coli exceeded the Basin Plan single sample numeric water quality standard for E. Coli density of 235/100ml for Fresh Waters Designated for Water Contact Recreation (REC-1).

4.20 c. **<u>pH:</u>** VCK's attached watershed monitoring program data indicates that on 6 out of 7 VCK monitoring events in the OID, pH levels in the OID water column exceeded the Basin Plan single sample numeric water quality standard of 8.5 for Fresh Waters Designated for Water Contact Recreation (REC-1).

4.21 d. **<u>Nitrate</u>:** VCK's attached watershed monitoring program data indicates that on 8 out of 8 VCK monitoring events at the OID, the concentration of Nitrate in the OID water column exceeded the numeric targets for Nitrate at 1 mg/l as derived in the Los Angeles Regional Water Quality Control Board's Machado Lake TMDL[10] and the Nutrient TMDL for Malibu

---

[8] J-Street Drain is visually depicted and labeled as an inland waterbody in Basin Plan Figure 2-1 :"Miscellaneous Streams and Coastal Features, Ventura County".

[9] The OID is visually depicted and labeled as an inland waterbody in Basin Plan Figure 2-1:"Miscellaneous Streams and Coastal Features, Ventura County".

[10] Resolution NO. R08-006, Amendment to the Water Quality Control Plan for the Los Angeles Region to Incorporate a Total Maximum Daily Load for Eutrophic, Algea, Ammonia, and Odors (Nutrient) for Machado Lake, California Regional Water Quality Control Board, Los Angeles Region. The Regional Board appropriately included a numeric target for total phosphorus of .1mg/l that was based of the EPA Nutrient Criteria Technical Guidance Manual Lakes and Reservoirs (2000), which does not recommend setting a numeric target for total phosphorus greater than 0.1 mg/L. Additionally, to maintain a balance of nutrients for biomass growth and prevent limitation by one nutrient or another, a ratio of total nitrogen to

Creek, adopted by USEPA in 2003[11]. In addition, it should be noted that the USEPA guidance value for CWA section 304(a) nutrient criteria specific to the Los Angeles Region (Ecoregion III) is 0.38 mg/l total nitrogen and 0.022 mg/l total phosphorus for protection of aquatic life and recreation.[12]

7.) Santa Clara River Estuary

4.22 a. **Trash:** VCK's attached watershed monitoring program data indicates that on 8 out of 8 VCK monitoring events at the Santa Clara River Estuary, the presence of trash pollution in the Santa Clara River Estuary exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL.

4.23 b. **Dissolved Oxygen:** The City of Ventura's Dissolved Oxygen recordings recorded for 24 hour periods by the City's North Sonde (SCR Sonde #1) and South Sonde (SCR Sonde #2)[13] stationed in the Santa Clara River Estuary, when converted to mg/l from % saturation based on additional water quality parameter recordings obtained by the City's sondes, violated the Basin Plan numeric water quality standard for Dissolved Oxygen of 5 mg/l for surface waters designated as WARM and 6mg/l for surface waters designated as COLD on over 40 days between 2009 and 2010.

4.24 c. **Nitrate:** VCK's attached watershed monitoring program data indicates that on 8 out of 10 VCK monitoring events at the Santa Clara River Estuary, the concentration of Nitrate in the Santa Clara River Estuary water column exceeded the numeric targets for Nitrate at 1 mg/l as derived in the Los Angeles Regional Water Quality Control Board's Machado Lake TMDL and the Nutrient TMDL for Malibu Creek, adopted by USEPA in 2003. In addition, it should be noted that the USEPA guidance value for CWA section 304(a) nutrient criteria specific to the Los Angeles Region (Ecoregion III) is 0.38 mg/l total nitrogen and 0.022 mg/l total phosphorus for protection of aquatic life and recreation.[14]

4.25 d. **Phosphate:** VCK's attached watershed monitoring program data indicates that on 10 out of 10 VCK monitoring events at the Santa Clara River Estuary, the concentration of Phosphate in the Santa Clara River Estuary water column exceeded the numeric targets for Phosphate at .1 mg/l as

---

total phosphorus of 10 is used to derive the total nitrogen numeric target of 1.0 mg/L as a monthly average concentration (Thomann, Mueller, 1987)." (Regional Board Staff Report for Machado Lake TMDL at 35.)

[11] The Nutrient TMDL for Malibu Creek, adopted by USEPA in 2003, provides summer season water quality objectives of 1.0 mg/l total nitrogen and 0.1 mg/l total phosphorous. Other established nitrogen criteria for protection of aquatic life are significantly lower.

[12] See: USEPA, *Ambient Water Quality Criteria Recommendations: Rivers and Streams in Nutrient Ecoregion III* (2000) (EPA 822-B-00-016).

[13] Data from City of Ventura included in email and attachments Labeled: City of Ventura Data

[14] See: USEPA, *Ambient Water Quality Criteria Recommendations: Rivers and Streams in Nutrient Ecoregion III* (2000) (EPA 822-B-00-016).

derived in the Los Angeles Regional Water Quality Control Board's Machado Lake TMDL and the Nutrient TMDL for Malibu Creek, adopted by USEPA in 2003. In addition, it should be noted that the USEPA guidance value for CWA section 304(a) nutrient criteria specific to the Los Angeles Region (Ecoregion III) is 0.38 mg/l total nitrogen and 0.022 mg/l total phosphorus for protection of aquatic life and recreation.[15]

4.26 e. **<u>pH:</u>** VCK's attached watershed monitoring program data indicates that on 2 VCK monitoring events, and on greater than 60 City of Ventura[16] pH recordings taken on separate days in the Santa Clara River Estuary via the City's North and South Sondes, pH levels in the Santa Clara River Estuary water column exceeded the Basin Plan single sample numeric water quality standard of 8.5 for Fresh Waters Designated for Water Contact Recreation (REC-1).

4.27 f. **<u>Low Flows:</u>** As discussed in the City of Ventura Estuary Special Studies One Year Assessment (attached) and the July 23, 2008, National Marine Fisheries Service, Southwest Region Final Biological Opinion (BIOP) concerning the operation of the Vern Freeman Diversion and Fish-Passage Facility (attached), due to diversions at the Vern Freeman Diversion Dam by United Water Conservation District, the Santa Clara River Estuary, Santa Clara River Reach 1, and Santa Clara River Reach 2 are deprived of sufficient flows during the wet season for Southern California Steelhead smolt and migrating adults to migrate up and down the Santa Clara River, and the Estuary does not receive sufficient flows during the dry season when the Estuary is closed as a lagoon to sustain aquatic life. Additionally, flow data indicates that reduced flows below the Vern Freeman Diversion Dam alters the natural flow regime needed to sustain aquatic life and vegetation that evolved with the River's natural flows. Attached daily flow data obtained from United Water Conservation District from 1993-2010, and monthly flow dating back to the 1956, above and below the Vern Freeman Diversion Dam, with the quantity of flows diverted by United included, demonstrates the flow impairments in the Santa Clara River Estuary, Santa Clara River Reach 1, and Santa Clara River Reach 2.

8.) Santa Clara River Reach 1

4.28 a. **<u>Low Flows:</u>** As discussed in the City of Ventura Estuary Special Studies One Year Assessment (attached) and the July 23, 2008, National Marine Fisheries Service, Southwest Region Final Biological Opinion (BIOP) concerning the operation of the Vern Freeman Diversion and Fish-Passage Facility (attached), due to diversions at the Vern Freeman Diversion Dam by United Water Conservation District, the Santa Clara River Estuary,

---

[15] See: USEPA, *Ambient Water Quality Criteria Recommendations: Rivers and Streams in Nutrient Ecoregion III* (2000) (EPA 822-B-00-016).

[16] Data from City of Ventura included in email and attachments Labeled: City of Ventura Data

Santa Clara River Reach 1, and Santa Clara River Reach 2 are deprived of sufficient flows during the wet season for Southern California Steelhead smolt and migrating adults to migrate up and down the Santa Clara River, and the Estuary does not receive sufficient flows during the dry season when the Estuary is closed as a lagoon to sustain aquatic life. Additionally, flow data indicates that reduced flows below the Vern Freeman Diversion Dam alters the natural flow regime needed to sustain aquatic life and vegetation that evolved with the River's natural flows. Attached daily flow data obtained from United Water Conservation District from 1993-2010, and monthly flow dating back to the 1956, above and below the Vern Freeman Diversion Dam, with the quantity of flows diverted by United included, demonstrates the flow impairments in the Santa Clara River Estuary, Santa Clara River Reach 1, and Santa Clara River Reach 2. Additionally, VCK attached watershed monitoring program data indicates no flow or trickle flow in the Santa Clara River at SC-02 below Highway 101, which would other wise be of greater magnitude or sufficient magnitude to support aquatic life absent a diversion at the Vern Freeman Diversion Dam.

4.29 b. **Trash:** VCK's attached watershed monitoring program data indicates that on 9 out of 9 VCK monitoring events at Santa Clara Reach 1, the presence of trash pollution in the Santa Clara River Reach 1 exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL.

9.) Santa Clara River Reach 2

4.30 a. **Low Flows:** As discussed in the City of Ventura Estuary Special Studies One Year Assessment (attached) and the July 23, 2008, National Marine Fisheries Service, Southwest Region Final Biological Opinion (BIOP) concerning the operation of the Vern Freeman Diversion and Fish-Passage Facility (attached), due to diversions at the Vern Freeman Diversion Dam by United Water Conservation District, the Santa Clara River Estuary, Santa Clara River Reach 1, and Santa Clara River Reach 2 are deprived of sufficient flows during the wet season for Southern California Steelhead smolt and migrating adults to migrate up and down the Santa Clara River, and the Estuary does not receive sufficient flows during the dry season when the Estuary is closed as a lagoon to sustain aquatic life. Additionally, flow data indicates that reduced flows below the Vern Freeman Diversion Dam alters the natural flow regime needed to sustain aquatic life and vegetation that evolved with the River's natural flows. Attached daily flow data obtained from United Water Conservation District from 1993-2010, and monthly flow dating back to the 1956, above and below the Vern Freeman Diversion Dam, with the quantity of flows diverted by United included, demonstrates the flow impairments in the Santa Clara River Estuary, Santa Clara River Reach 1, and Santa Clara River Reach 2.

4.31 b. **Fish Passage:** As discussed in the July 23, 2008, National Marine Fisheries Service, Southwest Region Final Biological Opinion (BIOP) concerning the operation of the Vern Freeman Diversion and Fish-Passage Facility (attached), the Vern Freeman Diversion Dam with its current fish ladder are a fish barrier to migrating Southern California Steelhead in Santa Clara River Reach 2 and 3.

10.) Santa Clara River Reach 3

4.32 a. **E. Coli**: VCK's attached watershed monitoring program data indicates that on 5 out of 27 VCK monitoring events at Santa Clara River Reach 3 on the Santa Clara River below the Santa Paula Creek confluence, on the Santa Clara River below the Sespe Creek Confluence, and on the lower segments of Sespe Creek and Santa Paula Creek, the presence of E. Coli in the water column of these waterbodies exceeded the Basin Plan single sample numeric water quality standard for E. Coli density of 235/100ml for Fresh Waters Designated for Water Contact Recreation (REC-1). Additionally, water monitoring on 11/26/08, 12/15/08, 2/6/2009, and 3/5/2009 at ME-SCR (attached), the mass emissions station sampling station operated by the Ventura County Watershed Protection District just above the Vern Freeman Diversion Dam, indicated E.Coli concentrations of 820/100ml, 4884/100ml, 12033/100ml, and 3873/100ml respectively (attached). All of these samples exceeding Basin Plan numeric water quality standards were taken by the county during wet weather events (see Ventura Annual Stormwater Report Appendix F starting at PDF pg 108).

4.33 b. **Trash:** VCK's attached watershed monitoring program data indicates that on 26 out of 31 VCK monitoring events at the Santa Clara River Reach 3 on the Santa Clara River below the Santa Paula Creek confluence, on the Santa Clara River below the Sespe Creek confluence, and on the lower segments of Sespe Creek and Santa Paula Creek, the presence of trash pollution in these waterbodies exceeded the numeric target for trash as derived in the Los Angeles River Trash TMDL.

4.34 c. **Fish Passage:** As discussed in the July 23, 2008, National Marine Fisheries Service, Southwest Region Final Biological Opinion (BIOP) concerning the operation of the Vern Freeman Diversion and Fish-Passage Facility (attached), the Vern Freeman Diversion Dam with its current fish ladder are a fish barrier to migrating Southern California Steelhead in Santa Clara River Reach 2 and 3.

11.) Santa Clara River Reach 4a

4.35 a. **Trash:** VCK's attached watershed monitoring program data indicates that on 7 out of 8 VCK monitoring events in the Santa Clara River Reach 4 below the Santa Clara River's confluence with Piru Creek, the presence of trash pollution exceeded the numeric target for trash in Santa Clara Reach 4 as derived in the Los Angeles River Trash TMDL.

12.) Santa Clara River Reach 5 or 6

4.36 a. **<u>Trash:</u>** VCK's attached watershed monitoring program data indicates that on 5out of 7 VCK monitoring events at the Santa Clara River Reach 5 or 6 in Santa Clarita (see attached long lat coordinates), the presence of trash pollution exceeded the numeric target for trash in Santa Clara River Reach 5 or 6 as derived in the Los Angeles River Trash TMDL.

Thank you for considering our data and agency data, and the incorporation of the above mentioned waterbodies as impaired for the above specified constituents into the 2012 California Integrated Report as Clean Water Act 303(d) impaired waterbodies. The ecological integrity and water quality of Ventura County's inland and coastal waterbodies would benefit greatly from these 303(d) listings for all of our communities.

Please feel free to contact us with any questions.

Sincerely,

Jason Weiner, M.E.M.
Associate Director & Staff Attorney
Ventura Coastkeeper
jweiner.venturacoastkeeper@wishtoyo.org
805-823-3301

These are the listings VCK specifically asked for listing in VCK's submission letter dated 8/30/2010
Date: March 23, 2017

Reach	**Pollutant**	**Data Source**	**RB Action**
Nicholas Canyon Creek (San Nicolas Canyon Ck)	Trash	VCK data	Data not assessed (5/7)
San Jon Barranca Creek (Sanjon Barranca Creek)	Trash	VCK data	Data not assessed (8/8)
	E coli	VCK data	Data not assessed (5/8)
Ormond Beach Lagoon (Ormond Beach Wetlands)	Trash	VCK data	Data not assessed (9/9)
	E coli	VCK data	**Do Not Delist (DI 42278) Data is not assessed.**
	pH (>8.5)	VCK data	Data not assessed (6/8)
	Nitrate(>1 mg/L or >10 mg/L)	VCK data	Data not assessed (VKC (11/14), RB(0/10))
Bubbling Springs (Hueneme Drain)	Trash	VCK data	Data not assessed (9/9)
	E coli	VCK data	Data not assessed (5/11)
J Street Drain	Trash	VCK data	List (DI 63443)
Oxnard Industrial Drain (Oxnard Drain)	Trash	VCK data	Data not assessed (8/8)
	Ecoli	VCK data	Data not assessed (VKC(5/11), RB(3/7))
	pH (>8.5)	VCK data	Data not assessed (VKC(6/7), RB(5/7)) **Do Not List (DI62330) Data is not assessed.**
	Nitrate(>1 mg/L or >10 mg/L)	VCK data	Data not assessed (VKC (8/8), RB(3/8))
Santa Clara River Estuary	Trash	VCK data	**Do Not List (DI66592) Data (2009) is used** Data not assessed (8/8)
	DO	City of Ventura Sonde data	**Do Not List (DI66590)** Problems QAQC
	Nitrate	VCK data	**List (DI35380)** Data not assessed (8/10)
	Phosphate	VCK data	Data not assessed (10/10)
	pH	VCK data	**List (DI66591)** Data not assessed
	Low flows	City of Ventura estuary special study	Flow, see below
Santa Clara Reach 1	Low flows	City of Ventura estuary special study	Flow, see below
	Trash	VCK data	**List (DI66631)**

			Data not assessed (9/9)
Santa Clara Reach 2	Low flows	City of Ventura estuary special study	Flow, see below
	Fish passage	NMFS BO	Flow, see below
Santa Clara Reach 3	E coli	VCK data	Data not assessed (5/27)
	Trash	VCK data	Data not assessed (26/31)
	Fish passage	NMFS BO	Flow, see below
Santa Clara Reach 4a	Trash	VCK data	Data not assessed (7/8)
Santa Clara Reach 5or6	Trash	VCK data	Data not assessed (5/7)

The Effects of Dissolved Oxygen on Steelhead Trout, Coho Salmon, and Chinook Salmon Biology and Function by Life Stage

Katharine Carter
Environmental Scientist
California Regional Water Quality Control Board
North Coast Region

August 2005

Introduction

Adequate concentrations of dissolved oxygen in fresh water streams are critical for the survival of salmonids. Fish have evolved very efficient physiological mechanisms for obtaining and using oxygen in the water to oxygenate the blood and meet their metabolic demands (WDOE 2002). However, reduced levels of dissolved oxygen can impact growth and development of different life stages of salmon, including eggs, alevins, and fry, as well as the swimming, feeding and reproductive ability of juveniles and adults. Such impacts can affect fitness and survival by altering embryo incubation periods, decreasing the size of fry, increasing the likelihood of predation, and decreasing feeding activity. Under extreme conditions, low dissolved oxygen concentrations can be lethal to salmonids.

Literature reviewed for this analysis included EPA guidance, other states' standards, reports that compiled and summarized existing scientific information, and numerous laboratory studies. When possible, species-specific requirements were summarized for the following life stages: migrating adults, incubation and emergence, and freshwater rearing and growth. The following information applies to salmonids in general, with specific references to coho, Chinook, steelhead, and other species of salmonids as appropriate.

Adult Migration

Reduced concentrations of dissolved oxygen can negatively affect the swimming performance of migrating salmonids (Bjornn and Reiser 1991). The upstream migration by adult salmonids is typically a stressful endeavor. Sustained swimming over long distances requires high expenditures of energy and therefore requires adequate levels of dissolved oxygen. Migrating adult Chinook salmon in the San Joaquin River exhibited an avoidance response when dissolved oxygen was below 4.2 mg/L, and most Chinook waited to migrate until dissolved oxygen levels were at 5 mg/L or higher (Hallock et al. 1970).

Incubation/Emergence

Low levels of dissolved oxygen can be directly lethal to salmonids, and can also have sublethal effects such as changing the rate of embryological development, the time to hatching, and size of emerging fry (Spence et al. 1996). The embryonic and larval stages of salmonid development are especially susceptible to low dissolved oxygen levels as their ability to extract oxygen is not fully developed and their relative immobility inhibits their ability to migrate to more favorable conditions. The dissolved oxygen requirements for successful incubation of embryos and emergence of fry is tied to intragravel dissolved oxygen levels. Intragravel dissolved oxygen is typically a function of many chemical, physical, and hydrological variables, including: the dissolved oxygen concentration of the overlying stream water, water temperature, substrate size and porosity, biochemical oxygen demand of the intragravel water, sediment oxygen demand, the gradient and velocity of the stream, channel configuration, and depth of water. As a result the dissolved oxygen concentration within the gravels can be depleted causing problems for salmonid embryos and larvae, even when overlying surface water oxygen levels are suitable (USEPA 1986).

Studies note that water column dissolved oxygen concentrations are typically estimated to be reduced by 1-3 mg/L as water is transmitted to redds containing developing eggs and larvae (WDOE 2002). USEPA (1986) concluded that dissolved oxygen levels within the gravels should be considered to be at least 3 mg/L lower than concentrations in the overlying water. ODEQ (1995) expect the loss of an average of 3 mg/L dissolved oxygen from surface water to the gravels.

Incubation mortality

Phillips and Campbell (1961, as cited by Bjornn and Reiser, 1991) concluded that intragravel dissolved oxygen must average 8 mg/L for embryos and alevins to survive well. After reviewing numerous studies Davis (1975) states that a dissolved oxygen concentration of 9.75 mg/L is fully protective of larvae and mature eggs, while at 8 mg/L the average member of the incubating population will exhibit symptoms of oxygen distress, and at 6.5 mg/L a large portion of the incubating eggs may be affected. Bjornn and Reiser (1991) reviewed numerous references and recommend that dissolved oxygen should drop no lower than 5 mg/L, and should be at or near saturation for successful incubation.

In a review of several laboratory studies, ODEQ (1995) concluded that at near optimum (10°C) constant temperatures acute mortality to salmonid embryos occurs at relatively low concentrations of dissolved oxygen, near or below 3 mg/L. Field studies reviewed by ODEQ (1995) demonstrate that embryo survival is low when the dissolved oxygen content in the gravels drops near or below 5 mg/L, and survival is greater at 8 mg/L.

Silver et al. (1963) performed a study with Chinook salmon and steelhead trout, rearing eggs at various constant dissolved oxygen concentrations and water velocities. They found that steelhead embryos held at 9.5°C and Chinook salmon embryos held at 11°C experienced complete mortality at dissolved oxygen concentrations of 1.6 mg/L. Survival of a large percentage of embryos reared at oxygen levels as low as 2.5 mg/L appeared to be possible by reduction of respiration rates and consequent reduction of growth and development rates.

In a field study Cobel (1961) found that the survival of steelhead embryos was correlated to intragravel dissolved oxygen in the redds, with higher survival at higher levels of dissolved oxygen. At 9.25 mg/L survival was 62%, but survival was only 16% at 2.6 mg/L. A laboratory study by Eddy (1971) found that Chinook salmon survival at 10.4 mg/L (13.5 °C) was approximately 67%, however at dissolved oxygen levels of 7.3 mg/L (13.5 °C) survival dropped to 49-57.6%. At temperatures more suitable for Chinook incubation (10.5 °C) Eddy (1971) found the percent survival remained high (over 90%) at dissolved oxygen levels from 11 mg/L to 3.5 mg/L; however, as dissolved oxygen levels decreased, the number of days to hatching increased and the mean dry weight of the fry decreased substantially. WDOE (2002) also points out that the studies above did not consider the act of emerging through the redds, and the metabolic requirements to emerge would be expected to be substantial. Therefore, it is likely that higher oxygen levels may be needed to fully protect hatching and emergence, than to just support hatching alone.

Incubation growth

Embryos can survive when dissolved oxygen is below saturation (and above a critical level), but development typically deviates from normal (Bjornn and Reiser, 1991). Embryos were found to be smaller than normal, and hatching either delayed or premature, when dissolved oxygen was below saturation throughout development (Doudoroff and Warren 1965, as cited by Bjornn and Reiser 1991).

Garside (1966) found the number of days it took for rainbow trout to go from fertilization to hatching increased as dissolved oxygen concentrations and water temperature decreased. In this study, rainbow trout were incubated at temperatures between 2.5 - 17.5°C and dissolved oxygen levels from 2.5 - 11.3 mg/L. At 10°C and 7.5°C the total time for incubation was delayed 6 and 9 days respectively at dissolved oxygen levels of 2.5 mg/L versus embryos incubated at approximately 10.5 mg/L.

Silver et al. (1963) found that hatching of steelhead trout held at 9.5°C was delayed 5 to 8 days at dissolved oxygen concentrations averaging 2.6 mg/L versus embryos reared at 11.2 mg/L. A smaller delay of hatching was observed at oxygen levels of 4.2 and 5.7 mg/L, although none was apparent at 7.9 mg/L. For Chinook salmon held at 11°C, Silver et al. observed that embryos reared at oxygen levels lower than 11 mg/L experienced a delay in hatching, with the most significant delay in those reared at dissolved oxygen levels of 2.5 mg/L (6 to 9 days). The size of both Chinook and steelhead embryos increased with increases in dissolved oxygen up to 11.2 mg/L. External examination of embryos revealed abnormal structural development in Chinook salmon tested at dissolved oxygen concentrations of 1.6 mg/L, and abnormalities in steelhead trout at concentrations of 1.6 and 2.6 mg/L. The survival of Chinook salmon after hatching was only depressed at the 2.5 mg/L level, the lowest level at which hatching occurred, with lower mortalities occurring at higher velocities. Post hatching survival of steelhead trout could not be determined due to numerous confounding factors.

Shumway et al. (1964) conducted a laboratory study to determine the influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. The experiments were conducted at a temperature of 10°C and oxygen levels generally ranging from 2.5 - 11.5 mg/L and flows from 3 to 750 cm/hour. It was concluded that the median time to hatching decreased and size of fry increased as dissolved oxygen levels increased. For example, steelhead trout embryos reared at 2.9 mg/L hatched in approximately 41 days and had a wet weight of 17 mg, while embryos reared at 11.9 mg/L hatched in 36 days and weighed 32.3 mg. The authors found that a reduction of either the oxygen concentration or the water velocity will reduce the size of fry and increase the incubation period, although the affect of various water velocities tested was less than the effect of the different dissolved oxygen concentrations tested.

WDOE (2002) reviewed various references and found that at favorable incubation temperatures a mean oxygen concentration of 10.5 mg/L will result in a 2% reduction in growth. At other oxygen concentrations, growth is reduced as follows: 8% reduction at oxygen levels of 9 mg/L, 10% reduction at 7 mg/L, and a 25% reduction at 6 mg/L.

Incubation avoidance/preference

Alevin showed a strong preference for oxygen concentrations of 8 - 10 mg/L and moved through the gravel medium to these concentrations, avoiding concentrations from 4 - 6 mg/L (WDOE 2002).

Emergence mortality

"The hatching time, size, and growth rate of developing embryos is proportional to the dissolved oxygen concentrations up to 8 mg/L or greater. The ability of fry to survive their natural environment may be related to the size of fry at hatch (ODEQ 1995)." McMahon (1983) recommends dissolved oxygen levels be ≥ 8 mg/L for high survival and emergence of fry. In a review of controlled field and lab studies on emergence, WDOE (2002) states that average intragravel oxygen concentrations of 6 - 6.5 mg/L and lower can cause stress and mortality in developing embryos and alevin. It is also noted that field studies on emergence consistently cite intragravel oxygen concentrations of 8 mg/L or greater as being associated with or necessary for superior health and survival, oxygen concentrations below 6 - 7 mg/L result in a 50% reduction in survival through emergence, and oxygen concentrations below 5 mg/L result in negligible survival. According to various laboratory studies, the threshold for complete mortality of emerging salmonids is noted to occur between 2 - 2.5 mg/L (WDOE, 2002).

After reviewing numerous literature sources, the USEPA (1986) concluded that the embryonic and larval stages of salmonid development will experience no impairment when water column dissolved oxygen concentrations are 11 mg/L. This translates into an intragravel dissolved oxygen concentration of 8 mg/L (USEPA assumes a 3 mg/L loss between the surface water and gravels). Table 1 from the USEPA (1986) lists the water column and intragravel dissolved oxygen concentrations associated with various health effects. These health affects range from no production impairment to acute mortality.

Table 1: Dissolved oxygen concentrations and their effects salmonid embryo and larval stages (USEPA, 1986).

Level of Effect	Water Column DO (mg/L)	Intragravel DO (mg/L)
No Production Impairment	11	8*
Slight Production Impairment	9	6*
Moderate Production Impairment	8	5*
Severe Production Impairment	7	4*
Limit to Avoid Acute Mortality	6	3*

* A 3 mg/L loss is assumed between the water column dissolved oxygen levels and those intragravel.

Freshwater Rearing and Growth

Swimming and activity

Salmonids are strong active swimmers requiring highly oxygenated waters (Spence 1996), and this is true during the rearing period when the fish are feeding, growing, and avoiding predation. Salmonids may be able to survive when dissolved oxygen concentrations are low (<5 mg/L), but growth, food conversion efficiency, and swimming performance will be adversely affected (Bjornn and Reiser 1991). Davis (1975) reviewed numerous studies and reported no impairment to rearing salmonids if dissolved oxygen concentrations averaged 9 mg/L, while at oxygen levels of 6.5 mg/L "the average member of the community will exhibit symptoms of oxygen distress", and at 4 mg/L a large portion of salmonids may be affected. Dahlberg et al. (1968) state that at temperatures near 20°C any considerable decrease in the oxygen concentration below 9 mg/L (the air saturation level) resulted in some reduction of the final swimming speed. They found that between dissolved oxygen concentrations of 7 to 2 mg/L the swimming speed of coho declined markedly with the decrease in dissolved oxygen concentration.

In a laboratory study, Davis et al. (1963) reported that the maximum sustainable swimming speeds of wild juvenile coho salmon were reduced when dissolved oxygen dropped below saturation at water temperatures of 10, 15, and 20°C. Air-saturation values for these dissolved oxygen concentrations were cited as 11.3, 10.2, and 9.2 mg/L respectively. They found that the maximum sustained swimming speeds (based on first and second swimming failures at all temperatures) were reduced by 3.2 - 6.4%, 5.9 - 10.1%, 9.9 - 13.9%, 16.7 - 21.2%, and 26.6 - 33.8% at dissolved oxygen concentrations of 7, 6, 5, 4, and 3 mg/L respectively. The authors also conducted tests on juvenile Chinook salmon and found that the percent reductions from maximum swimming speed at temperatures ranging from 11 to 15°C were greater than those for juvenile coho. At the dissolved oxygen concentrations listed above swimming speeds were decreased by 10%, 14%, 20%, 27%, and 38% respectively.

WDOE (2002) reviewed various data and concluded that swimming fitness of salmonids is maximized when the daily minimum dissolved oxygen levels are above 8 - 9 mg/L. Jones et al. (1971, as cited by USEPA 1986) found the swimming speed of rainbow trout was decreased 30% from maximum at dissolved oxygen concentrations of 5.1 mg/L and 14°C. At oxygen levels of

3.8 mg/L and a temperature of 22°C, they found a 43% reduction in the maximum swimming speed.

Growth

In a review of constant oxygen exposure studies WDOE (2002) concluded salmonid growth rates decreased less than 10% at dissolved oxygen concentrations of 8 mg/L or more, less than 20% at 7 mg/L, and generally less than 22% at 5 - 6 mg/L. Herrmann (1958) found that the mean percentage of weight gain in juvenile coho held at constant dissolved oxygen concentrations was 7.2% around 2 mg/L, 33.6% at 3 mg/L, 55.8% near 4 mg/L, and 67.9% at or near 5 mg/L. In a laboratory study Fischer (1963) found that the growth rates of juvenile coho exposed to constant oxygen concentrations ranging from 2.5 to 35.5 mg/L (fed to satiation, temperature at approximately 18 °C) dramatically decreased with decreases in the oxygen concentration below 9.5 mg/L (air saturation level). WDOE (2002) concludes that a monthly or weekly average concentration of 9 mg/L, and a monthly average of the daily minimum concentrations should be at or above 8 - 8.5 mg/L to have a negligible effect (5% or less) on growth and support healthy growth rates.

Food conversion efficiency is related to dissolved oxygen levels and the process becomes less efficient when oxygen concentrations are below 4 - 4.5 mg/L (ODEQ 1995). Bjornn and Reiser (1991) state that growth, food conversion efficiency, and swimming performance are adversely affected when dissolved oxygen concentrations are <5 mg/L. The USEPA (1986) reviewed growth data from a study conducted by Warren et al. (1973) where tests were conducted at various temperatures to determine the growth of coho and Chinook. USEPA cites that, with the exception of tests conducted at 22 °C, the results supported the idea that the effects of low dissolved oxygen become more severe at higher temperatures.

Brett and Blackburn (1981) performed a laboratory study to determine the growth rate and food conversion efficiency of young coho and sockeye salmon fed full rations. Tests were performed at dissolved oxygen concentrations ranging from 2 to 15 mg/L at a constant temperature of 15°C, the approximate optimum temperature for growth of Pacific Salmon. Both species showed a strong dependence of growth on the environmental oxygen concentrations when levels were below 5 mg/L. For coho, zero growth was observed at dissolved oxygen concentrations of 2.3 mg/L. The mean value for maximum coho growth occurred at 4 mg/L, and at dissolved oxygen concentrations above this level growth did not appear to be dependant on the dissolved oxygen. Sockeye displayed zero growth at oxygen levels of 2.6 mg/L, and reached the zone of independence (growth not dependant on dissolved oxygen levels) at 4.2 mg/L. Brett and Blackburn (1981) conclude that the critical inflection from oxygen dependence to independence occurs at 4 - 4.2 mg/L for coho and sockeye.

Herrmann et al. (1962) studied the influence of various oxygen concentrations on the growth of age 0 coho salmon held at 20 °C. Coho were held in containers at a constant mean dissolved oxygen level ranging from 2.1 - 9.9 mg/L and were fed full rations. The authors concluded that oxygen concentrations below 5 mg/L resulted in a sharp decrease in growth and food consumption. A reduction in the mean oxygen levels from 8.3 mg/L to 6 and 5 mg/L resulted in slight decreases in food consumption and growth. Weight gain in grams per gram of food consumed was slightly depressed at dissolved oxygen concentrations near 4 mg/L, and were markedly reduced at lower concentrations. At oxygen levels of 2.1 and 2.3 mg/L, many fish died and the surviving fish lost weight and consumed very little food.

USEPA (1986) calculated the median percent reduction in growth rate of Chinook and coho salmon fed full rations at various dissolved oxygen concentrations. They calculated no reduction in growth at dissolved oxygen concentrations of 8 and 9 mg/L, and a 1% reduction in growth at 7 mg/L for both species. At 6 mg/L Chinook and coho growth were reduced by 7% and 4% respectively. Dissolved oxygen levels of 4 mg/L result in a 29% reduction in growth for Chinook salmon and 21% reduction in growth for coho. At 3 mg/L there was a 47% decrease in Chinook growth and a 37% reduction in coho growth. USEPA (1986) states that due to the variability inherent in growth studies the reductions in growth rates seen above 6 mg/L are not usually statistically significant, while reductions in growth at dissolved oxygen levels below 4 mg/L are considered severe.

Avoidance and preference

Salmonids have been reported to actively avoid areas with low dissolved oxygen concentrations, which is likely a useful protective mechanism that enhances survival (Davis 1975). Field and laboratory studies have found that avoidance reactions in juvenile salmonids consistently occur at concentrations of 5 mg/L and lower, and there is some indication that avoidance is triggered at concentrations as high as 6 mg/L. Therefore these dissolved oxygen levels should be considered a potential barrier to the movement and habitat selection of salmonids (WDOE 2002).

Spoor (1990) performed a laboratory study on the distribution of fingerling brook trout in dissolved oxygen concentration gradients. Sixteen gradients between 1 and 8.9 mg/L were used for the study to determine what level of dissolved oxygen is preferred by the brook trout. It was found that in the absence of a gradient with dissolved oxygen concentrations at 6 mg/L or more throughout the system, the fish moved freely without showing preference or avoidance. Movement from low to higher oxygen concentrations were noted throughout the study. Fish moved away from water with dissolved oxygen concentrations from 1 - 1.9 mg/L within one hour, moved away from water with dissolved oxygen concentrations of 2 - 2.9 mg/L within 1 - 2 hours, and moved away more slowly from concentrations of 3 - 3.9 mg/L. From his study, Spoor (1996) concluded that brook trout will avoid oxygen concentrations below 4 mg/L, and preferred oxygen levels of 5 mg/L or higher.

Whitmore et al. (1960) performed studies with juvenile coho and Chinook salmon to determine their avoidance reaction to dissolved oxygen concentration of 1.5, 3 , 4.5, and 6 mg/L at variable river water temperatures. Juvenile Chinook salmon showed marked avoidance of oxygen concentrations near 1.5, 3, and 4.5 mg/L in the summer at mean temperatures ranging from 20.7 - 22.8°C, but no avoidance to levels near 6 mg/L at a mean temperature of 18.4°C. Chinook did not show as strong an avoidance to these oxygen levels in the fall when water temperatures were lower, ranging from 11.8 - 13.2°C. Chinook showed little avoidance of dissolved oxygen concentrations near 4.5 mg/L during the fall, and no avoidance to concentrations near 6 mg/L. In all cases avoidance became progressively larger with reductions in the oxygen concentration below 6 mg/L. Seasonal differences of avoidance are most likely due to differences in water temperature. At temperatures ranging from 18.4 - 19°C juvenile coho salmon showed some avoidance to all of the above oxygen concentrations, including 6 mg/L. Their behavior was more erratic than that of Chinook, and their avoidance of concentrations near 4.5 mg/L and lower was not as pronounced at corresponding temperatures. The juvenile coho often started upon entering water with low dissolved oxygen and then darted around until they found their way out of the experimental channel.

USEPA (1986) performed a literature review and cites the effects of various dissolved oxygen concentrations on salmonid life stages other than embryonic and larval (Table 2). These effects range from no impairment at 8 mg/L to acute mortality at dissolved oxygen levels below 3 mg/L.

Table 2: Dissolved oxygen concentrations and their effects on salmonid life stages other than embryonic and larval (USEPA, 1986).

Level of Effect	Water Column DO (mg/L)
No Production Impairment	8
Slight Production Impairment	6
Moderate Production Impairment	5
Severe Production Impairment	4
Limit to Avoid Acute Mortality	3

Lethality

Salmonid mortality begins to occur when dissolved oxygen concentrations are below 3 mg/L for periods longer than 3.5 days (US EPA 1986). A summary of various field study results by WDOE (2002) reports that significant mortality occurs in natural waters when dissolved oxygen concentrations fluctuate the range of 2.5 - 3 mg/L. Long-term (20 - 30 days) constant exposure to mean dissolved oxygen concentrations below 3 - 3.3 mg/L is likely to result in 50% mortality of juvenile salmonids (WDOE, 2002). According to a short-term (1 - 4 hours) exposure study by Burdick et al. (1954, as cited by WDOE, 2002), in warm water (20 - 21°C) salmonids may require daily minimum oxygen levels to remain above 2.6 mg/L to avoid significant (50%) mortality. From these and other types of studies, WDOE (2002) concluded that juvenile salmonid mortality can be avoided if daily minimum dissolved oxygen concentration remain above 3.9 mg/L, and the monthly or weekly average of minimum concentrations remains above 4.6 mg/L.

REFERENCES

Bjornn, T. and D. Reiser. 1991. Habitat requirements of salmonids in streams. In Meehan, W. ed., Influences of Forest and Rangeland Management on Salmonids Fishes and Their Habitat. American Fisheries Society Special Publication 19. pp. 83-138.

Brett, J. R., and J.M. Blackburn. 1981. Oxygen requirements for growth of young coho (*Oncorhynchus kisutch*) and sockeye (*O. nerka*) salmon at 15C. Can. J. Fish. Aquat. Sci. 38:399-404.

Cobel, D.W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. Transactions of the American Fisheries Society. 90:469-474.

Dahlberg, M.L., D.L. Shumway, and P. Doudoroff. 1968. Influence of dissolved oxygen and carbon dioxide on swimming performance of largemouth bass and coho salmon. Journal of the Fisheries Research Board of Canada. 25(1):49-70.

Davis, G.E., J. Foster, C.E. Warren, and P. Doudoroff. 1963. The influence of oxygen concentration on the swimming performance of juvenile pacific salmon at various temperatures. Transactions of the American Fisheries Society. 92:111-124.

Davis, J.C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on canadian species: a review. Journal of the Fisheries Research Board of Canada. 32:2295-2332.

Eddy, R.M. 1971. The influence of dissolved oxygen concentration and temperature on the survival and growth of Chinook salmon embryos and fry. Masters of Science Thesis. Oregon State University. Corvallis, Oregon. 45pp.

Fischer, R.J. 1963. Influence of Oxygen Concentration and of its Diurnal Fluctuations on the Growth of Juvenile Coho Salmon. Masters of Science Thesis. Oregon State University. Corvallis, Oregon. 48pp.

Garside, E.T. 1966. Effects of oxygen in relation to temperature on the development of embryos of brook trout and rainbow trout. J. Fish. Res. Bd. Canada 23(8)1121-1134.

Hallock, R.J., R.F. Elwell, and D.H. Fry, Jr. 1970. Migrations of adult king salmon *Oncorhynchus tshawytsca* in the San Joaquin Delta as demonstrated by the use of sonic tags. California Department of Fish and Game, Fish Bulletin 151. 92pp.

Herrmann, R.B. 1958. Growth of juvenile coho salmon at various concentrations of dissolved oxygen. Masters of Science Thesis. Oregon State University. Corvallis, Oregon. 82pp.

Herrmann, R.B., C.E. Warren, and P. Doudoroff. 1962. Influence of oxygen concentration on the growth of juvenile coho salmon. Transactions of the American Fisheries Society. 91:155-167.

McMahon, T.E. 1983. Habitat suitability index models: Coho salmon. U.S. Department of Interior, Fish and Wildlife Service. FWS/OBS-82/10.49. 29pp.

Oregon Department of Environmental Quality (ODEQ). 1995. Dissolved Oxygen: 1992-1994 Water quality standards review. Final Issue Paper. 166pp. Available online at: <http://www.fishlib.org/Bibliographies/waterquality.html>. Website accessed August 20, 2004.

Shumway, D.L., C.E. Warren, and P. Doudoroff. 1964. Influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. Transactions of the American Fisheries Society. 93:342-356.

Silver, S.J., C.E. Warren, P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and Chinook salmon embryos at different water velocities. Transactions of the American Fisheries Society. 92(4):327-343.

Spence, B.C., and G.A. Lomnicky, R.M. Hughs, and R.P. Novitzki. 1996. An ecosystem approach to salmonid conversation. TR-4501-96-6057. ManTech Environmental Research Services Corp., Corvallis, Oregon. Available from the National Marine Fisheries Service, Portland, Oregon.

Spoor, W.A. 1990. Distribution of fingerling brook trout, ,*Salvelinus fontinalis* (Mitchill), in dissolved oxygen concentration gradients. J. Fish. Biol. 36:363-373.

U.S. Environmental Protection Agency (USEPA). 1986. Ambient Water Quality Criteria for Dissolved Oxygen. Office of Water. EPA 440/5-86-003. 35pp. Available online at: <http://www.epa.gov/cgi-bin/claritgw?op-Display&document=clserv:OAR:0579;&rank=4&template=epa>. Website accessed July 5, 2004.

Washington State Department of Ecology (WDOE). 2002. Evaluating Criteria for the Protection of Freshwater Aquatic Life in Washington's Surface Water Quality Standards: Dissolved Oxygen. Draft Discussion Paper and Literature Summary. Publication Number 00-10-071. 90pp.

Whitmore, C.M., C.E. Warren, and P. Doudoroff. 1960. Avoidance reactions of salmonid and centrarchid fishes to low oxygen concentrations. Transactions of the American Fisheries Society. 89:17-26.

Appendix 4

Effects of Temperature, Dissolved Oxygen/Total Dissolved Gas, Ammonia, and pH on Salmonids

Implications for California's North Coast TMDLs

Katharine Carter
Environmental Scientist
North Coast Regional Water Quality Control Board

July 2008

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1. TEMPERATURE

1.1 Introduction

Temperature is one of the most important environmental influences on salmonid biology. Most aquatic organisms, including salmon and steelhead, are poikilotherms, meaning their temperature and metabolism is determined by the ambient temperature of water. Temperature therefore influences growth and feeding rates, metabolism, development of embryos and alevins, timing of life history events such as upstream migration, spawning, freshwater rearing, and seaward migration, and the availability of food. Temperature changes can also cause stress and lethality (Ligon et al. 1999). Temperatures at sub-lethal levels can effectively block migration, lead to reduced growth, stress fish, affect reproduction, inhibit smoltification, create disease problems, and alter competitive dominance (Elliott 1981, USEPA 1999a). Further, the stressful impacts of water temperatures on salmonids are cumulative and positively correlated to the duration and severity of exposure. The longer the salmonid is exposed to thermal stress, the less chance it has for long-term survival (Ligon et al. 1999).

A literature review was performed to evaluate temperature needs for the various life stages of steelhead trout (*Oncorhynchus mykiss*), coho salmon (*Oncorhynchus kisutch*), and Chinook salmon (*Oncorhynchus tschawytscha).* The purpose of this review was to identify temperature thresholds that are protective of salmonids by life stage, as a basis for evaluating stream temperatures in California temperature TMDLs within the North Coast region.

This review included USEPA temperature guidance, Oregons' and Washingtons' temperature standards reviews, reports that compiled and summarized existing scientific information, and laboratory and field studies. When possible, species-specific needs were summarized by the following life stages: migrating adults, spawning and incubation/emergence, and freshwater rearing and growth. Additionally, the effects of temperature on disease and lethality are also discussed. Some of the references reviewed covered salmonids as a general class of fish, while others were species specific. Information for fall run coho salmon, spring/summer, fall, and winter steelhead, and spring and fall run Chinook salmon are compiled by life stage in Table 1 through Table 12.

1.2 Temperature Metrics

In considering the effect of temperature on salmonids, it is useful to have a measure of chronic and acute (i.e. sub-lethal and lethal) temperature exposures. A common measure of chronic exposure is the maximum weekly average temperature (MWAT). The MWAT is the maximum seasonal or yearly value of the mathematical mean of multiple, equally spaced, daily temperatures over a running seven-day consecutive period (Brungs and Jones 1977, p.10). In other words, it is the highest single value of the seven-day moving average temperature. A common measure of acute effects is the instantaneous maximum. A third metric, the maximum weekly maximum temperature (MWMT), can be used as a measure of both chronic and acute effects. The MWMT is also known as the seven-day average of the daily maximum temperatures (7-DADM), and is the maximum seasonal or yearly-value of the daily maximum temperatures over a running seven-day consecutive period. The MWMT is useful because it describes the maximum temperatures in a stream, but is not overly influenced by the maximum temperature of a single day.

Much of the information reported in the literature characterizes temperature needs with terms such as “preferred” or “optimum”. Preferred stream temperatures are those that fish most frequently inhabit when allowed to freely select temperatures in a thermal gradient (USEPA 1999a). An optimum range provides suitable temperatures for feeding activity, normal physiological response, and normal behavior (without symptoms of thermal stress) (USEPA 1999a). Optimal temperatures have also been described as those temperatures at which growth rates, expressed as weight gain per unit of time, are maximal for the life stage (Armour 1991).

Salmonid stocks do not tend to vary much in their life history thermal needs, regardless of their geographic location. In the 2001 USEPA document, *Summary of Technical Literature Examining the Physiological Effects of Temperature on Salmonids,* the case is made that there is not enough significant genetic variation among stocks or among species of salmonids to warrant geographically specific water temperature standards.

> Climate conditions vary substantially among regions of the State and the entire Pacific Northwest. …Such [varying climatic] conditions could potentially have led to evolutionary adaptations, resulting in development of subspecies differences in thermal tolerance. …[However,] the literature on genetic variation in thermal effects indicates occasionally significant but very small differences among stocks and increasing differences among subspecies, species, and families of fishes. Many differences that had been attributed in the literature to stock differences are now considered to be statistical problems in analysis, fish behavioral responses under test conditions, or allowing insufficient time for fish to shift from field conditions to test conditions (Mathur & Silver 1980, Konecki et al. 1993, both as cited in USEPA 2001).

Additionally:

> There are many possible explanations why salmonids have not made a significant adaptation to high temperature in streams of the Pacific Northwest. Temperature tolerance is probably controlled by multiple genes, and consequently would be a core characteristic of the species not easily modified through evolutionary change without a radical shift in associated physiological systems. Also, the majority of the life cycle of salmon and steelhead is spent in the ocean rearing phase, where the smolt, subadults, and adults seek waters with temperatures less than 59°F (15°C) (Welch et al, 1995, as cited in USEPA 2001).

As a result, literature on the temperature needs of coho and Chinook salmon and steelhead trout stemming from data collected in streams outside Northern California are cited in this document and are considered relevant to characterizing the thermal needs of salmonids, which use Northern California rivers and streams.

1.3 Adult Migration and Holding

All of the adult migration and holding temperature needs referenced in this section can be found in Table 1 through Table 3. Salmon and trout respond to temperatures during their upstream migration (Bjornn and Reiser 1991). Delays in migration have been observed in response to temperatures that were either too cold or too warm. Most salmonids have evolved with the temperature regime they historically used for migration and spawning, and deviations from the normal pattern can affect survival (Spence et al. 1996).

In a 2003 USEPA document entitled *EPA Region 10 Guidance for Pacific Northwest State and Tribal Water Quality Standards*, it is recommended that the 7-DADM should not exceed 18°C in waters where both adult salmonid migration and “non-core” juvenile rearing occur during the period of summer maximum temperatures. The document does not define what constitutes the “summer” period. Non-core juvenile rearing is defined as moderate to low density salmon and trout rearing usually occurring in the mid or lower part of the basin, as opposed to areas of high density rearing which are termed “core” rearing areas. This criterion is derived from analysis and synthesis of past laboratory and field research. The USEPA believes that this temperature recommendation will protect against lethal conditions, prevent migration blockage, provide optimal or near optimal juvenile growth conditions, and prevent high disease risk by minimizing the exposure time to temperatures which can lead to elevated disease rates.

A 7-DADM temperature of 20°C is recommended by the USEPA (2003) for waterbodies that are used almost exclusively for migration during the period of summer maximum temperatures.

> EPA believes that a 20°C criterion would protect migrating juveniles and adults from lethal temperatures and would prevent migration blockage conditions. However, EPA is concerned that rivers with significant hydrologic alterations (e.g., rivers with dams and reservoirs, water withdrawals, and /or significant river channelization) may experience a loss of temperature diversity in the river, such that maximum temperatures occur for an extended period of time and there is little cold water refugia available for fish to escape maximum temperatures. In this case, even if the river meets a 20°C criterion for maximum temperatures, the duration of exposure to 20°C temperatures may cause adverse effects in the form of increased disease and decreased swimming performance in adults, and increased disease, impaired smoltification, reduced growth, and increased predation for late emigrating juveniles…(USEPA 2003).

Therefore, the USEPA recommends a narrative provision to protect and, if possible, restore the natural thermal regime accompany the 7-DADM 20°C criterion for rivers with significant hydrologic alterations.

In an exhaustive study of both laboratory and field studies of temperature effects on salmonids and related species, USEPA (1999a, 2001) concluded that temperatures of approximately 22-24°C limit salmonid distribution, i.e., they totally eliminate salmonids from a location. USEPA (1999a) also notes that changes in competitive interactions between fish species can lead to a transition in dominance from salmonids to other species at temperatures 2-4°C lower than the range of total elimination.

1.3.1 Steelhead Trout Migration

In a 2002 review of numerous studies, Washington State Department of Ecology (WDOE) concluded that daily average temperatures of 21-24°C are associated with avoidance behavior and migration blockage in steelhead trout. WDOE suggests that the MWMT should not exceed 17-18°C, and daily maximum temperatures should not exceed 21-22°C to be fully protective of adult steelhead migration.

Table 1: Effects of Temperature in Considering Adult Steelhead and Migration

C	MIGRATION		
24	21-24 Average daily temperature associated with avoidance and migration blockage (2)	22-24 Temperature range which eliminates salmonids from an area (3,4)	
23			
22		21-22 Daily maximum temperature should not exceed this to be fully protective (2)	18-22 Temperature range at which transition in dominance from salmonids to other species occurs (4)
21			
20	20 MWMT should not exceed this in waterbodies used almost exclusively for migration. Should be used in conjunction with a narrative provision about protecting/restoring the natural thermal regime for rivers with significant hydrologic alterations (1)		
19			
18	17-18 MWMT should not exceed this to be fully protective (2)	18 MWMT should not exceed this where migration and non-core rearing occur (1)	
17			

Sources: (1) USEPA 2003, (2) WDOE 2002, (3) USEPA 2001, (4) USEPA 1999a

1.3.2 Chinook Salmon Migration and Holding

USEPA (2001) cited various literature sources that identified thermal blockages to Chinook salmon migration at temperatures ranging from 19-23.9°C, with the majority of references citing migration barriers at temperatures around 21°C.

A radio tracking study on spring Chinook revealed that when maximum temperatures of 21.1°C were reached, a thermal barrier to migration was established (Bumgarner et al. 1997, as cited by USEPA 1999a). Bell (1986) reviewed various studies and notes spring Chinook migrate at water temperatures ranging from 3.3-13.3°C, while fall Chinook migrate at temperatures of 10.6-19.6°C. Preferred temperatures for Chinook range from 7.2-14.5°C (Bell 1986). Based on a technical literature review, WDOE (2002) concluded that daily maximum temperatures should not exceed 21-22°C during Chinook migration.

Table 2: Effects of Temperature in Considering Adult Chinook and Migration and Holding

°C	MIGRATION				
24			22-24 Temperature range which eliminates salmonids from an area (3,5)	19-23.9 Range of temperatures causing thermal blockage to migration (3)	
23	23 Klamath Basin fall Chinook begin migration upstream at temperatures as high as 23C if temperatures are rapidly falling (6)				
22	22 Klamath Basin fall Chinook will not migrate upstream when mean daily temperatures are 22C or greater (6)				18-22 Temperature range at which transition in dominance from salmonids to other species occurs (5)
21	21-22 Daily maximum temperature should not exceed this range to be protective of migration (2)		21 Most references cite as thermal block to migration (3) 21 Klamath Basin fall Chinook will not migrate upstream if temperatures are 21C or above and rising (6)		
20	20 MWMT should not exceed this in waterbodies used almost exclusively for migration. Should be used in conjunction with a narrative provision about protecting/restoring the natural thermal regime for rivers with significant hydrologic alterations (1)				
19			10.6-19.6 Temperature range where adult fall Chinook migrate (4)		
18				18 MWMT should not exceed this where migration and non-core rearing occur (1)	
17	16-17 MWMT should be below this where Chinook are holding (2)				
16					
15					
14	7.2-14.5 Preferred temperatures for Chinook (4)			13-14 Average daily temperature should be below this where spring Chinook are holding (2)	
13					
12				3.3-13.3 Temperature range where adult spring Chinook migrate (4)	
11					
10					
9					
8					
7					
6					
5					
4					
3					

Sources: (1) USEPA 2003, (2) WDOE 2002, (3) USEPA 2001, (4) Bell 1986, (5) USEPA 1999a, (6) Strange 2006

Utilizing radio telemetry to track the movements and monitor the internal body temperatures of adult fall Chinook salmon during their upriver spawning migration in the Klamath basin, Strange (2006) found that fall Chinook will not migrate upstream when mean daily temperatures are ≥22°C. Strange also noted that adult fall Chinook in the

Klamath basin will not migrate upstream if temperatures are 21°C or above and rising, but will migrate at temperatures as high as 23°C if temperatures are rapidly falling.

Spring Chinook begin entering freshwater streams during a relatively cool-water season but must hold throughout the warm summer period, awaiting cooler spawning temperatures (ODEQ 1995a). The cumulative effects of management practices such as elevated water temperatures, reduced cover from large woody debris, and reduced resting pool area due to pool filling increase the susceptibility of holding adult fish to mortality from thermal effects (The Oregon Department of Environmental Quality [ODEQ] 1995a). WDOE states that where spring Chinook are holding over for the summer prior to spawning the average daily water temperature should be below 13-14°C and the MWMT should be below 16-17°C (WDOE 2002).

1.3.3 Coho Salmon Migration

Migration for coho is delayed when water temperatures reach 21.1°C, and the preferred water temperatures for coho range from 11.7-14.5°C (Bell 1986). In California coho salmon typically migrate upstream when water temperatures range from 4-14°C (Briggs, 1953 and Shapovalov and Taft, 1954, as cited by Hassler, 1987). WDOE reviewed various studies and concluded that to be protective of adult coho migration, MWMTs should not exceed 16.5°C (WDOE 2002).

Table 3: Effects of Temperature in Considering Adult Coho and Migration

<table>
<tr><th>°C</th><th colspan="3">MIGRATION</th></tr>
<tr><td>24</td><td colspan="2" rowspan="3">22-24 Temperature range which eliminates salmonids from an area (3,6)</td><td></td></tr>
<tr><td>23</td><td></td></tr>
<tr><td>22</td><td rowspan="5">18-22 Temperature range at which transition in dominance from salmonids to other species occurs (6)</td></tr>
<tr><td>21</td><td colspan="2">21.1 Migration is delayed when temperatures reach this value (4)</td></tr>
<tr><td>20</td><td colspan="2">20 MWMT should not exceed this in waterbodies used almost exclusively for migration. Should be used in conjunction with a narrative provision about protecting/restoring the natural thermal regime for rivers with significant hydrologic alterations (1)</td></tr>
<tr><td>19</td><td colspan="2"></td></tr>
<tr><td>18</td><td colspan="2">18 MWMT should not exceed this where migration and non-core rearing occur (1)</td></tr>
<tr><td>17</td><td colspan="3"></td></tr>
<tr><td>16</td><td colspan="3">16.5 MWMT should not exceed this value to be fully protective (2)</td></tr>
<tr><td>15</td><td colspan="3"></td></tr>
<tr><td>14</td><td rowspan="4">11.7-14.5 Preferred temperature range (4)</td><td colspan="2" rowspan="5">4-14 Temperature range at which migration typically occurs (5)</td></tr>
<tr><td>13</td></tr>
<tr><td>12</td></tr>
<tr><td rowspan="2">11</td></tr>
<tr><td>11.4 Preferred temperature (7)</td></tr>
</table>

Sources: (1) USEPA 2003, (2) WDOE 2002, (3) USEPA 2001, (4) Bell 1986, (5) Briggs 1953, Shapovalov and Taft 1954, as cited by Hassler 1987, (6) USEPA 1999a, (7) Reutter and Herdendorf 1974

1.4 Spawning, Incubation, and Emergence

All of the spawning, incubation, and emergence temperature needs referenced in this section can be found in Table 4 through Table 7. Many sources have stated that temperature affects the time of migration i adults and thus the time of spawning, which influences the incubation temperature regime, which in turn influences survival rates, development rates, and growth of embryos and alevins (Murray and McPhail 1988). USEPA Region 10 recommends that the 7-DADM temperatures should not exceed 13°C for salmonid spawning, egg incubation, and fry emergence (USEPA 2003). Optimum temperatures for salmonid egg survival ranges from 6-10°C (USEPA 2001).

1.4.1 Steelhead Spawning, Incubation, and Emergence

In a discussion paper and literature summary evaluating temperature criteria for fish species including salmonids and trout, WDOE (2002) cites studies showing that steelhead were observed spawning in temperatures ranging from 3.9-21.1°C, and that the preferred temperatures for steelhead spawning range from 4.4-12.8°C. In a review of various studies, Bell (1986) concludes that steelhead spawning occurs at water temperatures ranging from 3.9-9.4°C.

Steelhead and rainbow trout eggs had the highest survival rates between 5-10°C according to Myrick and Cech (2001), and while they can tolerate temperatures as low as 2°C or as high as 15°C, mortality is increased at these temperatures. WDOE (2002) reviewed literature on the survival of steelhead and rainbow trout embryos and alevins at various temperatures and concluded that the average water temperature should not exceed 7-10°C throughout development, and the maximum daily average temperature should be below 11-12°C at the time of hatching (WDOE 2002).

Table 4: Effects of Temperature in Considering Steelhead Incubation and Emergence

°C	**INCUBATION AND EMERGENCE**		
15	15 Steelhead and rainbow trout eggs can survive at temperatures as high as this but mortality is high compared to lower temperatures (3)		
14			
13	13 MWMT should not exceed this value to be protective of spawning, egg incubation, and fry emergence (1)		
12	11-12 Maximum daily average temperature should be below this range at the time of hatching (2)		
11			
10	5-10 Steelhead and rainbow trout eggs had the highest survival within this range (3)	6-10 Optimum temperature for salmonid eggs survival to hatching (4)	7-10 Average daily temperature should not exceed this range throughout embryo development (2)
9			
8			
7			
6			
5			
4			
3			
2	2 Steelhead and rainbow trout eggs can survive at temperatures as low as this but mortality is high compared to higher temperatures (3)		

Sources: (1) USEPA 2003, (2) WDOE 2002, (3) Myrick and Cech 2001, (4) USEPA 2001

Table 5: Effects of Temperature in Considering Steelhead, Chinook, and Coho Spawning

°C	Steelhead			Chinook			Coho		All Salmonids
21	3.9-21.2 Steelhead observed spawning in this temp. range (2)								
20									
19									
18									
17						5.6-17.7 Range of temps. associated with spawning from references reviewed (2)			
16									
15				13-15.5 Temp. range at which pre-spawning mortality becomes pronounced in ripe spring Chinook (4)					
14					14.5 Majority of refs. cite daily max temps. associated with spawning below this level (2)				
13					5.6-13.9 Recommended temperature range for spawning (5)		13 Daily maximum temp. not to exceed this value to be protective (6)	4.4-13.3 Typical temps. during which spawning occurs (2)	13 MWMT not exceed this value during spawning, egg incubation, and fry emergence (1)
12			4.4-12.8 Preferred temp. range for spawning (2)	5.6-12.8 Recom-mended temperature range for spawning (4)					
11									
10							10 MWAT not exceed this value to be protective (6)		
9		3.9-9.4 Temp. range where spawning occurs (3)					4.5-9.4 Preferred spawning temperature range (3)		
8									
7									
6									
5									
4									
3									

Sources: (1) USEPA 2003, (2) WDOE 2002, (3) Bell 1986, (4) ODEQ 1995a, (5) Reiser and Bjornn 1979 as cited by Armour et al. 1991, (6) Brungs and Jones 1977

1.4.2 Chinook Spawning, Incubation, and Emergence

ODEQ (1995a) reviewed numerous studies and recommended a temperature range of 5.6-12.8°C for spawning Chinook. A discussion paper and literature summary by WDOE in 2002 found that the literature reviewed noted a wide range of temperatures associated with Chinook spawning (5.6-17.7°C), although the majority of these temperature observations cite daily maximum temperatures below 14.5°C. A spawning temperature range of 5.6-13.9°C is recommended for spring, summer, and fall Chinook salmon populations in the Pacific Northwest (Reiser and Bjornn 1979, as cited by Armour et al. 1991). When ripe adult spring Chinook females experience temperatures above 13-15.5°C, pre-spawning adult mortality becomes pronounced (ODEQ 1995a). Additionally, there is decreased survival of eggs to the eyed stage and alevin development is inhibited due to the exposure of the ripe female to warm temperatures, even if the stream temperatures during the egg and alevin development are appropriate (ODEQ 1995a).

Table 6: Effects of Temperature in Considering Chinook Incubation and Emergence

°C	**INCUBATION AND EMERGENCE**					
20	17.5-20 The highest single day maximum temperature should not exceed this range to protect eggs and embryos from acute lethal conditions (2)					
19						
18						
17						
16						1.7-16.7 Eggs can survive these temps. but mortality is greatly increased at the extremes (3)
15						
14	5-14.4 Recom-mended temp. range for incubation (4)	13.5-14.5 Daily maximum temperatures should not exceed this from fertilization through initial fry development (5)	14 Moderate embryo survival (6)		2-14 Range of temps. for normal embryo develop-ment (6)	
13			13 MWMT should not exceed this value to be protective of spawning, egg incubation, and fry emergence (1)			
12			4-12 Lowest levels of egg mortality at these temps. (3)	11-12.8 Average daily temperatures should be below this range at beginning of incubation (2)		
11		11 High embryo survival (6)				
10		9-10 Optimal temp. should be below this range (5)		6-10 Optimum temperature for salmonid eggs survival to hatching (5)		
9		8-9 Seasonal ave. temps. should not exceed this range from fertilization through initial fry development (2)				
8		8 High embryo survival (6)				
7						
6						
5		5 High embryo survival (6)				
4						
3						
2	2 Poor embryo survival (6)					
1						

Sources: (1) USEPA 2003, (2) WDOE 2002, (3) Myrick and Cech 2001, (4) Reiser and Bjornn 1979, as cited by Armour et al. 1991, (5) USEPA 2001, (6) Murray and McPhail 1988

WDOE (2002) reviewed numerous references on the effects of various temperatures on Chinook incubation and development and used these studies to derive the temperatures that are protective of Chinook salmon from fertilization through fry development. These reviewed references include laboratory studies assessing Chinook embryo survival at various constant temperatures, studies attempting to mimic naturally fluctuating temperatures experienced by incubating eggs, studies which have made stepwise reductions in the incubation temperatures as incubation progressed to evaluate survival of eggs, and studies on the effects of transferring eggs to optimal constant incubation temperatures after they had been exposed to higher temperatures for various periods. As a result of this review, WDOE (2002) recommends that average daily temperatures remain below 11-12.8°C at the initiation of incubation, and that the seasonal average should not exceed 8-9°C in order to provide full protection from fertilization through initial fry development. The highest single day maximum temperature should not exceed 17.5-20°C to protect eggs and embryos from acute lethal conditions (WDOE 2002).

USEPA (2001) reviewed multiple literature sources and concluded that optimal protection from fertilization through initial fry development requires that temperatures be maintained below 9-10°C, and that daily maximum temperatures should not exceed 13.5-14.5°C. Reiser and Bjornn (1979, as cited by Armour et al. 1991) recommended temperatures of 5.0-14.4°C for spring, summer and fall Chinook salmon incubation in the Pacific Northwest. Myrick and Cech (2001) reviewed studies on the Sacramento-San Joaquin River and concluded that the lowest levels of Chinook egg mortality occurred at temperatures between 4-12°C, and while eggs can survive at temperatures from 1.7-16.7°C, mortality is greatly increased at the temperature extremes.

Embryo survival was studied in a laboratory experiment conducted by Murray and McPhail (1988). They incubated five species of Pacific salmon, including Chinook, at five incubation temperatures (2, 5, 8, 11, 14°C). Chinook embryo survival was high at 5, 8, and 11°C, but survival was moderate at 14°C and poor at 2°C. As a result of their study, Murray and McPhail concluded that the range of temperatures for normal embryo development is > 2°C and <14°C (Murray and McPhail 1988).

1.4.3 Coho Spawning, Incubation, and Emergence

In 2002, WDOE found that several studies and literature reviews state that spawning activity in coho may typically occur in the range of 4.4-13.3ºC. According to a review by Bell (1986), preferred spawning temperatures range from 4.5-9.4ºC. Brungs and Jones (1977) used existing data on the optimum and range of temperatures for coho spawning and embryo survival to create criteria using protocols from the National Academy of Sciences and National Academy of Engineering. The resultant criteria were that the MWAT should not exceed 10ºC and the daily maximum temperature should not exceed 13ºC to be protective of coho (Brungs and Jones 1977, p.16).

In a discussion paper and literature summary WDOE (2002) reviewed studies that assessed the survival of embryos and alevin at various temperatures. Based on the findings of these studies WDOE (2002) has determined that the average daily temperature during the incubation period should be at or below 8-10ºC to fully support this coho salmon life stage. According to a review of various literature sources by Bell

(1986), the preferred emergence temperatures for coho range from 4.5-13.3ºC. USEPA (2001) concluded that to fully support pre-emergent stages of coho development MWMTs should not exceed 9-12°C.

Table 7: Effects of Temperature in Considering Coho Incubation and Emergence

<table>
<tr><th>°C</th><th colspan="5">INCUBATION AND EMERGENCE</th></tr>
<tr><td>**14**</td><td colspan="5">14 Upper limit for normal embryo development (5)</td></tr>
<tr><td>**13**</td><td colspan="3">13 MWMT should not exceed this value to be protective of spawning, egg incubation, and fry emergence (1)</td><td>13 Daily maximum temperature should not exceed this value to be protective (6)</td><td rowspan="11">4.5-13.3 Preferred emergence temperature range (3)</td></tr>
<tr><td>**12**</td><td colspan="2"></td><td rowspan="4">9-12 MWMT should not exceed this range to be fully protective (4)</td><td></td></tr>
<tr><td>**11**</td><td colspan="2"></td><td></td></tr>
<tr><td>**10**</td><td rowspan="5">6-10 Optimum temperature for salmonid eggs survival to hatching (4)</td><td rowspan="3">8-10 Ave. daily temp. during incubation should be at or below this to be supportive (2)</td><td>10 MWAT should not exceed this to be protective (6)</td></tr>
<tr><td>**9**</td><td></td></tr>
<tr><td>**8**</td><td></td><td></td></tr>
<tr><td>**7**</td><td colspan="3"></td></tr>
<tr><td>**6**</td><td colspan="3"></td></tr>
<tr><td>**5**</td><td></td><td colspan="3"></td></tr>
<tr><td>**4**</td><td></td><td colspan="3"></td></tr>
</table>

Sources: (1) USEPA 2003, (2) WDOE 2002, (3) Bell 1986, (4) USEPA 2001, (5) Murray and McPhail 1988, (6) Brungs and Jones 1977

Murray and McPhail (1988) incubated five species of Pacific salmon, including coho, at five temperatures (2, 5, 8, 11, 14°C) to determine embryo survival at various temperatures. Coho embryos suffered increased mortality above 11°C although survival was still high. They concluded that the upper limit for normal coho embryo development is 14°C (Murray and McPhail 1988).

1.5 Freshwater Rearing and Growth

All of the freshwater rearing and growth temperature needs referenced in this section can be found in Table 8 through Table 10. Temperature affects metabolism, behavior, and survival of both juvenile fish as well as other aquatic organisms that may be food sources. In streams of the Northern California Coast, including the Klamath River, young Chinook, coho and steelhead may rear in freshwater from one to four years before migrating to the ocean.

In an exhaustive study of both laboratory and field studies of temperature effects on salmonids and related species, USEPA (1999a) concluded that temperatures of approximately 22-24°C limit salmonid distribution, i.e., they totally eliminate salmonids from a location. USEPA (1999a) also notes that changes in competitive interactions between fish species can lead to a transition in dominance from salmonids to other species at temperatures 2-4°C lower than the range of total elimination.

To protect salmon and trout during summer juvenile rearing the USEPA (2003) for Region 10 provided a single guidance metric designating 16°C as the 7-DADM temperature that should not be exceeded in areas designated as “core” rearing locations. Core rearing areas are defined as areas with moderate to high densities of summertime salmonid juvenile rearing generally found in the mid- to upper portions of river basins. This criterion will protect juvenile salmonids from lethal temperatures, provide optimal to upper optimal conditions for juvenile growth depending on the time of year, avoid temperatures where salmonids are at a competitive disadvantage with other fish species, protect against increased disease rates caused by elevated temperatures, and provide temperatures which salmonids prefer according to scientific studies.

1.5.1 Steelhead Freshwater Rearing and Growth

Nielsen et al. (1994) studied thermally stratified pools and their use by juvenile steelhead in three California North Coast rivers including the Middle Fork Eel River, Redwood Creek at Redwood National Park, and Rancheria Creek, located in the Navarro River watershed. In detailed observations of juvenile steelhead behavior in and near thermally stratified pools in Rancheria Creek, Nielsen et al. (1994) noted behavioral changes including decreased foraging and increased aggressive behavior as pool temperature reached approximately 22°C. As pool temperature increased above 22°C, juveniles left the observation pools and moved into stratified pools where temperatures were lower.

Wurtsbaugh and Davis (1977, as cited by USEPA 2001) found that steelhead trout growth could be enhanced by temperature increases up to 16.5°C. Using a risk assessment approach which took into account “realistic food estimates”, Sullivan et al. (2000) report temperatures of 13-17.0°C (MWAT), 14.5-21°C (MWMT), and 15.5-21°C (annual maximum) will ensure no more than a 10% reduction from maximum growth for steelhead. Reduction from maximum growth will be ≤20% for temperatures ranging from 10-19.0°C (MWAT), 10-24°C (MWMT), and 10.5-26°C (annual maximum).

A literature review was conducted by WDOE (2002) in which studies to determine the water temperature that would allow for maximum growth of steelhead trout were analyzed. These included laboratory studies conducted at constant and fluctuating temperatures. One of the studies was conducted using feeding rates comparable to those observed in natural creeks, although most of the laboratory studies were conducted under satiated feeding conditions. As a result of this review of laboratory studies conducted at constant temperatures, WDOE (2002) concludes that under satiated rations growth may be maximized at temperatures as high as 17.2-19°C. Results from laboratory studies using variable temperatures show maximum growth occurs at average daily temperatures between 15.5-18°C, and that under feeding rates similar to natural conditions at various times of the year maximum growth rates occurred at mean temperatures of 13.3°C (spring season), 15.2°C (fall season) and 16.2°C (summer season).

Table 8: Effects of Temperature in Considering Juvenile Steelhead Rearing and Growth

°C	REARING AND GROWTH					
26						21-26 Annual maximum temp. which will ensure no more than 20% reduction from max. growth (4)
25						
24	22-24 Temperature range which totally eliminates salmonids from area, limiting their distribution (6)				21-24 MWMT which will ensure no more than 20% reduction from max growth (4)	
23		>22 Juveniles left observation pools and moved to pools with lower temperatures (2)				
22		22 Decreased foraging, increased aggressive behavior (2)		18-22 Temperature range at which transition in dominance from salmonids to other species occurs (6)		
21					14.5-21 MWMT which will ensure no more than 10% reduction from maximum growth (4)	15.5-21 Annual maximum temperature which will ensure no more than 10% reduction from maximum growth (4)
20						
19		17-19 MWAT will ensure no more than 20% reduction from max. growth (4)	17.2-19 Growth may be maximized at temperatures as high as this under satiated feeding conditions, lab studies at constant temperature (5)			
18				15.5-18 Average daily temperatures at which maximum growth occurs under satiated feeding, lab studies at varying temps (5)		
17		13-17 MWAT range which will ensure no more than 10% reduction from maximum growth (4)				
16	16.5 Growth enhanced by temp. increases up to this temp. (3) 16.2 Mean temp. at which max. growth occurred during the summer, lab studies using natural feeding conditions and varying temps. (5)		16 MWMT should not exceed this value to be protective of core rearing locations (1)			
15	15.2 Mean temp. at which max. growth occurred during the fall, lab studies using natural feeding conditions and varying temps. (5)					10.5-15.5 Annual maximum temperature which will ensure no more than 20% reduction from maximum growth (4)
14					10-14.5 MWMT which will ensure no more than 20% reduction from maximum growth (4)	
13	13.3 Mean temp. at which max. growth occurred during the spring, lab studies using natural feeding conditions and varying temps. (5)	10-13 MWAT will ensure no more than 20% reduction from maximum growth (4)				
12						
11						
10						

Sources: (1) USEPA 2003, (2) Nielsen et al. 1994, (3) Wurtsbaugh and Davis 1977, as cited by USEPA 2001, (4) Sullivan et al. 2000, (5) WDOE 2002, (6) USEPA 1999a

1.5.2 Chinook Freshwater Rearing and Growth

In a laboratory study, Brett (1952) demonstrated that juvenile Chinook salmon, acclimated to a temperature of 20°C, selectively aggregated in areas where the temperature was in the region of 12-13°C.

ODEQ (1995a), reviewed numerous studies and concluded for juvenile spring Chinook salmon rearing, positive growth takes place at temperatures between 4.5-19°C, and that optimum rearing production is between 10.0-15.6°C. However, as the extremes of this temperature range are reached growth reaches zero. Above and below these thresholds growth becomes negative as feeding ceases and respiration rates increase and/or decrease rapidly.

After synthesizing data from several sources USEPA (2001), came up with the same recommended optimum temperature zone for all Chinook salmon as ODEQ (1995a) of 10.0-15.6°C. While there is research suggesting that some Chinook stocks exhibit adequate rearing capabilities above 15.6°C, USEPA (2001) conclude that anything over this threshold significantly increases the risk of mortality from warm-water diseases.

In a laboratory study Marine and Cech (2004) studied the incremental effects of chronic exposure to three temperature regimes (13-16 °C, 17-20 °C, and 21-24 °C) on Chinook juveniles during rearing and smoltification. Their findings reflected that Chinook juveniles reared at the 17-20 ºC and 21-24 ºC temperature ranges experienced significantly decreased growth rates, impaired smoltification indices, and increased predation vulnerability compared with juveniles reared at 13-16 ºC.

In a field study Chinook grew faster in a stream where temperatures peaked at 16°C compared to a stream where temperatures peaked at 20°C (ODFW 1992, as cited by WDOE 2002). WDOE (2002) reviewed literature on Chinook growth including laboratory studies conducted at a constant temperature, laboratory studies conducted at fluctuating temperatures, and field studies to evaluate the water temperature that would be protective of Chinook and allow for maximum growth. Most of the laboratory studies were conducted under satiated feeding conditions, although one of the studies was conducted using feeding rates more comparable to those observed in natural creeks. As a result of this review of laboratory studies conducted at constant temperatures, WDOE (2002) concludes that maximum growth is expected to occur with exposure to constant temperatures from 15.6-19°C. However, increased growth at temperatures above 15.6°C was inconsistently greater, and under natural rations the temperatures at which maximum growth occurs may decline by as much as 4.2°C. Recommendations based on the review of two laboratory studies conducted at fluctuating temperatures are that "…average temperatures below 19°C are necessary to support maximum growth rates in Chinook salmon, and that the average temperature that produces maximum growth rates likely lies between 15-18°C (median 16.5°C)".

Table 9: Effects of Temperature in Considering Juvenile Chinook Rearing and Growth

°C	**REARING AND GROWTH**				
24	22-24 Temperature range which totally eliminates salmonids from area, limiting their distribution (7)			21-24 Decreased growth, impaired smoltification, increased predation compared to juveniles reared at 13-16 (6)	
23					
22			18-22 Temperature range at which transition in dominance from salmonids to other species occurs (7)		
21				17-20 Decreased growth, impaired smoltification, increased predation compared to juveniles reared at 13-16 (6)	
20					
19	19 Temperatures above this do not support maximum growth, lab studies at varying temperatures (3)	15.6-19 Maximum growth expected according to lab studies conducted at constant temperature and satiated rations. Under natural feeding conditions maximum growth may occur at temperatures as much as 4.2C lower (3)			4.5-19 Temperature range at which positive growth takes place (5)
18	15-18 Average temperature where maximum growth occurs, lab studies conducted at varying temperatures (3)				
17					
16			16 Chinook grew faster in a stream where temperatures peaked at 16 than when they peaked at 19C (3) 16 MWMT should not exceed this value to be protective of core rearing locations (2)	13-16 Increased growth, unimpaired smoltification, lower predation compared to juveniles reared at 21-24, or 17-20 (6)	
15	10-15.6 Temperature range for optimal growth. Anything over this threshold increases the risk of mortality from warm water disease (1)		10-15.6 Optimal temperature range for rearing (5)		
14					
13					
12				12-13 Juvenile Chinook acclimated to 20 selectively aggregate to these water temperatures (4)	
11					
10					
9					
8					
7					
6					
5					
4					

Sources: (1) USEPA 2001, (2) USEPA 2003, (3) WDOE 2002, (4) Brett 1952, (5) ODEQ 1995a, (6) Marine and Cech 2004, (7) USEPA 1999a

1.5.3 Coho Freshwater Rearing and Growth

In a study of juvenile coho presence and absence in the Mattole watershed, Welsh et al. (2001) used logistic regression to determine that an MWAT greater than 16.8°C or a MWMT greater than 18.1°C may preclude the presence of juvenile coho salmon in the stream. The criterion correctly determined the presence or absence of juvenile coho in 18 of 21 streams. Welsh et al. (2001) also reported that juvenile coho were found in all streams with an MWAT less than 14.5°C, or a MWMT less than 16.3°C.

Sullivan et al. (2000) reviewed sub-lethal and acute temperature thresholds from a wide range of studies, incorporating information from laboratory-based research, field observations, and risk assessment approaches. Using a risk assessment approach based on "realistic food estimates" Sullivan et al (2000) suggest that MWATs ranging from 12.5-14.5°C for coho will result in no more than a 10% reduction from maximum growth, and that a range for the MWAT of 9-18.5°C will reduce growth no more than 20% from maximum. Sullivan et al. (2000) also calculated temperature ranges for MWMT (13-16.5°C) and the annual maximum temperature (13-17.5°C) that will result in no more than a 10% reduction in maximum growth. They further calculated ranges for MWMT (9-22.5°C) and the annual maximum temperature (9.5-23°C) that will result in no more than a 20% growth loss.

In an attempt to determine the water temperature that will allow for maximum growth of coho salmon, WDOE (2002) reviewed literature on laboratory studies conducted at a constant temperature and fluctuating temperatures, and field studies. The two laboratory studies reviewed were conducted under satiated feeding conditions. Shelbourn (1980, as cited by WDOE 2002) found that maximum growth occurred at a constant temperature of 17°C, while Everson (1973, as cited by WDOE 2002) tested fish at different temperatures and determined that coho had the greatest growth at the temperature test regime from 12.1-20.8°C (median 16.5°C). While the various field studies reviewed did not provide an estimate of the temperature best for maximum growth they did allow for WDOE (2002) to conclude that weekly average temperatures of 14-15°C were more beneficial to growth than lower temperature regimes, and daily maximum temperatures of 21-26°C were detrimental to growth.

Brett (1952) acclimated five different species of salmon to various temperatures ranging from 5-24°C and found that coho salmon showed the greatest preference for temperatures between 12-14°C. It was also determined that coho showed a general avoidance of temperatures above 15°C even in fish who were acclimated to temperatures as high as 24°C.

Konecki et al. (1995a) raised two groups of juvenile coho salmon under identical regimes to test the hypothesis that the group from a stream with lower and less variable temperature would have a lower and less variable preferred temperature than the group from a stream with warmer and more variable temperatures. Results reflected that the two groups tended to differ in their preferred temperature range as predicted above, but the differences were slight. Konecki et al. (1995a) concluded that the temperature preference of juvenile coho salmon in their study was 10-12°C.

Table 10: Effects of Temperature in Considering Juvenile Coho Rearing and Growth

°C	REARING AND GROWTH				
26	21-26 Daily maximum temperatures in this range are detrimental to growth, according to field studies (3)				
25					
24			22-24 Temperature range which totally eliminates salmonids from an area, limiting their distribution (9)		
23					17.5-23 Annual maximum temperature will ensure no more than 20% reduction from maximum growth (2)
22			16.5-22.5 MWMT will ensure no more than 20% reduction from maximum growth (2)	18-22 Temperature range at which transition in dominance from salmonids to other species occurs (9)	
21					
20		12.1-20.8 Greatest growth occurs in this temperature range under satiated conditions, lab study (7)			
19					
18	18.1 MWMT above this may preclude the presence of juvenile coho in steams (5)				
17	14.5-18.5 MWAT will ensure no more than 20% reduction from maximum growth (2)			17 Maximum growth at this constant temperature, at satiated rations in a lab study (6)	13.5 17.5 Annual maximum temperature will ensure no more than 10% reduction from maximum growth (2)
16			13-16.5 MWMT will ensure no more than 10% reduction from maximum growth (2)	16.8 MWAT above this may preclude the presence of juvenile coho in streams (5) 16.3 Juveniles found in all streams with MWMT less than this value (5) 16 MWMT not exceed this value to be protective of core rearing locations (1)	
15				>15 Juveniles show avoidance, even those acclimated to 24C (4) 14-15 Weekly average temperatures in this range are more beneficial than lower temperatures (3)	
14	14.5 Juvenile coho found in all streams with MWAT less than this value (5)			12-14 Preferred temperature range (4)	
13	12.5-14.5 MWAT will ensure no more than 10% reduction from maximum growth (2)		9-13 MWMT will ensure no more than 20% reduction from maximum growth (2)		9.5-13.5 Annual maximum temperature will ensure no more than 20% reduction from max. growth (2)
12	9-12.5 MWAT will ensure no more than 20% reduction from maximum growth (2)			10-12 Preferred temperature range (8)	
11					
10					
9					

Sources: (1) USEPA 2003, (2) Sullivan et al. 2000, (3) WDOE 2002, (4) Brett 1952, (5) Welsh et al. 2001, (6) Shelbourn 1980, as cited by WDOE 2002, (7) Everson 1973, as cited by WDOE 2002, (8) Konecki et al. 1995a, (9) USEPA 1999a

1.6 Lethality

All of the lethal temperatures referenced in this section can be found in Table 11. WDOE (2002) reviewed literature on three types of studies (constant exposure temperature studies, fluctuating temperature lethality studies, and field studies) and used this information to calculate the MWMT that, if exceeded, may result in adult and juvenile salmonid mortality. The resultant MWMTs for these various types of studies are as follows: constant exposure studies 22.64°C, fluctuating lethality studies 23.05°C , and field studies 22.18°C.

1.6.1 Steelhead Lethality

Coutant (1970, as cited by USEPA 1999a) found that Columbia River steelhead, which were acclimated to a river temperature of 19°C, had a lethal threshold of 21°C. Bell (1986) reviewed various studies and states that the lethal threshold for steelhead is 23.9°C. According to the California Department of Fish and Game (2001, p.419), temperatures of 21.1°C have been reported as being lethal to adults.

1.6.2 Chinook Lethality

In a laboratory study, Brett (1952) acclimated five different species of juvenile salmon to various temperatures ranging from 5-24°C. At temperatures of 24°C and below there was 100% survival of fish during the one-week duration of the experiment. Brett (1952) concluded that the lethal temperature (temperature where survival becomes less than 100%) was between 24.0 and 24.5°C, and the ultimate upper lethal temperature was 25.1°C (temperature at which 50% of the population is dead after infinite exposure). A review of numerous studies led Bell (1986) to conclude that the upper lethal temperature for Chinook is 25°C. Myrick and Cech (2001) reviewed literature on studies from the Central Valley and found data to suggest that the chronic (exposure >7 days) upper lethal limit for juvenile Chinook is approximately 25°C.

1.6.3 Coho Lethality

In a review of various literature sources, Bell (1986) found that the upper lethal temperature for coho is 25.6°C. Brett (1952) concluded that the ultimate upper lethal temperature of juvenile coho salmon was 25.0°C (temperature at which 50% of the population is dead after infinite exposure). Thomas et al. (1986) conducted a study to determine the mortality of coho subjected to fluctuating temperatures. It was determined that the LT50 (the temperature at which 50% of the population will die) for fish acclimated to a 10-13°C cycle was 26°C for presmolts (age-2 fish), and 28°C for age-0 fish.

Table 11: Effects of Temperature in Considering Lethality and Salmonids

°C	Steelhead	Chinook	Coho	All Salmonids
28			28 LT50[1] for age 0-fish acclimated to a 10-13C cycle (6)	
27				
26			26 LT50[1] for presmolts (age 2-fish) acclimated to a 10-13C cycle (6)	
25		25.1 Upper lethal temp. at which 50% of the population would die after infinite exposure, juvenile Chinook acclimated to temperatures from 5-24C (4)	25.6 Upper lethal threshold (3)	
		25 Upper lethal threshold (3)	25 Upper lethal temp. at which 50% of the population would die after infinite exposure, juvenile coho acclimated to temps. from 5-24C (4)	
		25 Chronic (exposure >7 days) upper lethal limit for juvenile Chinook (5).		
24		24-24.5 Survival becomes less than 100% for juvenile Chinook acclimated to temperatures from 5-24C (4)		
23	23.9 Upper lethal threshold for steelhead (3)			23.05 do not exceed this value to prevent adult and juvenile mortality, data from fluctuating temp. studies (1)
22				22.64 do not exceed this value to prevent adult and juvenile mortality, data from constant exposure studies (1)
				22.18 do not exceed this value to prevent adult and juvenile mortality, data from field studies (1)
21	21.1 Temperature lethal to adults (7)			
	21 Lethal threshold for steelhead acclimated to 19C (2)			

[1] Maximum temperature in the cycle at which 50% mortality occurred

Sources: (1) WDOE 2002, (2) Coutant 1970, as cited by USEPA 1999a, (3) Bell 1986, (4) Brett 1952, (5) Myrick and Cech 2001, (6) Thomas et al. 1986, (7) California Department of Fish and Game (CDFG) 2001

1.7 Disease

All of the effects of temperatures on disease risk in salmonids referenced in this section can be found in Table 12. WDOE (2002) reviewed studies of disease outbreak in salmonids and estimates that an MWMT of less than or equal to 14.38°C (midpoint of 12.58-16.18 range) will virtually prevent warm water disease effects. To avoid serious

Table 12: Effects of Temperature in Considering Disease and Salmonids

°C	Ich		Ceratomyxosis		Columnaris	Disease (general)	
26		21-26.7 Optimum temp. range for Ich, compilation of temps. from three references (3,4,5)					
25							
24	>24 Lifecycle takes less than 4 days (5)						
23	21-23.9 Life cycle takes as few as 3-4 days (5)		23.3 Juvenile coho salmon and rainbow trout time from exposure to death is 12.5 and 14 days respectively (9)	6.7-23.3 Juvenile rainbow trout have little or no ability to overcome infection, and mortality varied from 75-86% (9)	23.3 Juvenile spring Chinook mortality was 92%, and time from exposure to death was 2.3 days (13)		
22					22.2 Mortality is 100% in juvenile sockeye exposed to *C. columnaris* (10)		
21	18.3-21.2 Serious outbreaks of Ich occur (4)				>21.1 Temperatures at this level are associated with a 28-74% infection rate in Chinook (11)		
20		20 Lifecycle takes 1 week (6)	20.5 Mortality is 84% in juvenile coho exposed to *C. shasta* (9).		20.5 Mortality in juvenile steelhead and coho from Columnaris was 100%, and 70% in juvenile spring Chinook (13) 20.5 In juvenile steelhead and coho time from exposure to death was 1.6-1.7 days (13) 20 Average water temperature at which low virulence strains show signs of outbreak (3, 12)	>20.88 MWMTs over this value can result in severe infections and catastrophic outbreaks (1)	18-20 Temperature range which is associated with a high risk of disease in rearing juveniles and migrating adults (2)
19							
18							
17					17.8 Mortality rates were 52, 92, and 99% for juvenile spring Chinook, steelhead and coho respectively (13)	17.38 MWMT should not be exceeded to avoid serious rates of infection and mortality (1)	14-17 Temperature range which is associated with an elevated risk of disease in rearing juveniles and migrating adults (2)
16					16.1 Mortality is 30% in juvenile sockeye exposed to *C. columnaris* (10)		
15	>15.6 Associated with outbreaks in salmonid fingerlings, especially Chinook (3) 15.5 Lifecycle of Ich takes 2 weeks (5)		15 Mortality is 22% in juvenile coho exposed to *C. shasta* (9).		15.6 Average water temperature at which low virulence strains show signs of outbreak (3) 15 Mortality was 31, 56, and 51% for juvenile spring Chinook, steelhead, and coho respectively (13)		
14						14.38 MWMT will virtually prevent all warm water disease (1)	

Table 12 (continued):Effects of Temperature in Considering Disease and Salmonids

°C	Ich	Ceratomyxosis		Columnaris	Disease (general)
13			6.7-23.3 Juvenile rainbow trout have little or no ability to overcome infection, and mortality varied from 75-86% (9)		12-13 Temperature range which minimizes the risk of disease in rearing juveniles and migrating adults (2)
12				12.8 After 7 days of infection mortality is 60-100% (majority of tests 100%) (12)	
				12.2 Mortality was 4-20% in juvenile spring Chinook, steelhead, and coho respectively. Time from exposure to death ranged from 7.6-12.2 days (13).	
11		10-11 *C. shasta* appears to be come infective (4)			
10	10 Lifecycle takes more than 5 weeks (5)				
		<10 Steelhead show evidence of *C. shasta* in ~38 days (8)			
9		9.4 Juvenile coho time from exposure to death is 146 days, mortality is 2% (9)		3.9-9.4 No mortality in spring Chinook, steelhead, or coho from Columnaris (13)	
8					
7	7 Lifecycle takes 20 days (6)				
	<7 Lifecycle takes more than 5 weeks (7)				
6					
			6.7 Juvenile rainbow trout time from exposure to death is 155 days (9)		
			3.9-6.7 No mortality in Juvenile coho exposed to *C. shasta* (9)		
5					
4					
3					

Sources: (1) WDOE 2002, (2) USEPA 2003, (3) Bell 1986, (4) CDWR 1988, (5) Piper et al 1982, (6) Nigrelli et al. 1976, as cited by Dickerson et al. 1995, (7) Durborow et al. 1998, (8) Leitritz and Lewis, 1976, (9) Udey et al. 1975, (10) Ordal and Rucker 1944, as cited by Pacha et al. 1970, (11) USEPA 1999a, (12) Pacha et al. 1970, (13) Holt et al. 1975 rates of infection and mortality the MWMT should not exceed 17.38°C (midpoint of 15.58-19.18 range), and that severe infections and catastrophic outbreaks become a serious concern when the MWMTs exceed 20.88°C (midpoint of 18.58-23.18 range).

In a summary of temperature considerations, USEPA (2003) states that disease risks for juvenile rearing and adult migration are minimized at temperatures from 12-13°C, elevated from 14-17°C, and high at temperatures from 18-20°C.

Acknowledging that there are many diseases that affect salmonids, the following discussion will focus on three which are common in the Klamath Basin: Ichthyophthiriasis (Ich), Ceratomyxosis, and Columnaris. *Ichthyophthirius multifiliis* is a protozoan parasite that causes the disease known as Ichthyophthiriasis (Ich). The disease ceratomyxosis is caused by a parasite, *Ceratomyxa shasta* (*C. shasta*). Columnaris disease is a bacterial infection caused by *Flavobacterium columnare* (synomyms*: Bacillus columnaris, Chondrococcus columnaris, Cytophaga columnaris, Flexibacter columnaris*).

1.7.1 Ichthyophthiriasis (Ich)

Nigrelli et al. (1976, as cited by Dickerson et al. 1995) proposed that there are physiological races of Ich, which are related to the temperature tolerance of the host fishes. Thus, there are races of Ich that infect cold-water (7.2-10.6°C) fishes such as salmon, and others that infect warm-water (12.8-16.1°C) tropical fishes. Bell (1986) discusses Ich and states that at water temperatures above 15.6°C, this disease often breaks out in salmon fingerlings, especially Chinook. CDWR (1988) states that serious outbreaks of Ich occur at temperatures from 18.3-21.2°C.

Numerous studies and reviews have been conducted on the optimal temperature for Ich. Piper et al. (1982, p.316.) wrote that optimal temperatures range from 21-23.9°C. CDWR (1988) stated the optimum temperature for Ich is in the range of 25 to 26.7°C, while Bell (1986) states optimum temperatures are noted from 21.2-26.7°C.

Temperature is an important factor in the persistence of Ich infections in salmonids. The growth period varies from 1 week at 20 °C to 20 days at 7 °C (Nigrelli et al. 1976, as cited by Dickerson et al. 1995). Piper et al. (1982, p.316) state that at optimal temperatures of 21-23.9°C, the life cycle may take as few as 3-4 days. The cycle requires 2 weeks at 15.5°C, and more than 5 weeks at 10°C (Piper et al. 1982, p.316). Durborow et al. (1998) note that to complete its lifecycle, Ich requires from less than 4 days at temperatures higher than 24°C, to more than 5 weeks at temperatures lower than 7°C. Although studies report varying lengths of time for Ich to complete its lifecycle at similar temperatures, it is clear that the speed at which Ich develops increases as temperatures increase.

1.7.2 Ceratomyxosis

In reviewing the literature on Ceratomyxosis (a disease caused by the parasite, C. shasta), it is clear that as water temperatures increase, the intensity of the disease increases, and the incubation period decreases (CDWR 1988, Letritz and Lewis, Udey et al. 1975). At water temperatures greater than 10°C, steelhead will show evidence of Ceratomyxosis in approximately 38 days (Leitritz and Lewis 1976, p.154). In a study of juvenile coho salmon by Udey et al. (1975), time from exposure to death was more than 90% temperature dependent, and increased from 12.5 days at 23.3°C, to 146 days at 9.4°C. These results show the accelerating effect of higher temperatures on the progress of the disease. The time from exposure to death of juvenile rainbow trout was nearly 97% temperature dependent, increasing from 14 days at 23.3°C to 155 days at 6.7°C (Udey et al. 1975).

C. shasta appears to become infective at temperatures around 10-11°C (CDWR 1988). According to Leitritz and Lewis (1976, p.154), steelhead from the Klamath River are quite susceptible to *C. shasta* infections and suffer severe losses when exposed.

Udey et al. (1975) conducted a study to determine the relation of water temperature to Ceratomyxosis in juvenile rainbow trout and coho salmon. Rainbow trout from the Roaring River Hatchery, and coho from Fall Creek Salmon Hatchery (both in Oregon) were used in this experiment. Groups of 25 fish exposed to *C. shasta* were transferred to 12.2°C water, and then were tempered to one of eight experimental temperatures from 3.9 to 23.3°C (2.8°C increments).

In the juvenile coho salmon experiment, Udey et al. (1975) found that percent mortality increased progressively from 2% at 9.4°C to 22% at 15.0°C and 84% at 20.5°C. No deaths occurred in coho salmon maintained at 3.9 and 6.7°C, indicating that ceratomyxosis in coho can be suppressed by water temperatures of 6.7°C or below (Udey et al. 1975).

Tests conducted by Udey et al. (1975) on rainbow trout juveniles indicate that once infection is initiated, juvenile rainbow trout have little or no ability to overcome *C. shasta* infections at water temperatures between 6.7 and 23.3°C. Fatal infections varied from 75-86% at temperatures ranging from 6.7 to 15.0°C (Udey et al. 1975). Mortality in trout held at 20.5 and 23.3°C were lower (72% and 52% respectively) due to losses from *Flexibacter columnaris*, which occurred well before the onset of deaths caused by *C. shasta*, in spite of efforts to control it with terramycin (Udey et al. 1975). The results from Udey et al. (1975) also reflected no deaths occurred in juvenile trout held at 3.9°C.

1.7.3 Columnaris

The importance of temperature on infections of Columnaris has been demonstrated in numerous laboratory studies. Ordal and Rucker (1944, as cited by Pacha et al. 1970) exposed juvenile sockeye salmon to *C. columnaris* and studied the effect of temperature on the disease. In these studies, the overall mortality ranged from 30% in fish held at 16.1°C to 100% in those held at 22.2°C (Ordal and Rucker 1944, as cited by Pacha et al. 1970). USEPA (1999a) cites studies that conducted surveys of Columnaris infection frequency on Chinook in the Snake River in July and early August of 1955-1957, which revealed 28-75% of fish infected when water temperature was >21.1°C.

Low virulence strains of Columnaris show signs of outbreak when average water temperatures are over 20°C (Bell 1986, Pacha et al. 1970). Bell (1986) states that outbreaks of high virulence strains occur when average water temperatures reach 15.6°C, and Pacha et al. (1970) found mortalities of 60-100% (majority of tests 100%) occur at temperatures of 12.8°C after 7 days of infection. With regard to strains of higher virulence, while these strains are capable of beginning infection and producing disease at water temperatures as low as 12.8°C, the disease process becomes progressively slower as the water temperature is lowered (Pacha et al. 1970).

Holt et al. (1975) performed a study on the relation of water temperature to Columnaris in juvenile steelhead trout and juvenile coho and spring Chinook salmon. Tests were performed on groups of 25-35 fish at eight temperatures ranging from 3.9°C to 23.3°C (2.8°C increments). At 20.5°C mortality was 100% in juvenile steelhead trout and coho salmon, 70% in juvenile spring Chinook salmon, and at temperatures 23.3°C juvenile spring Chinook mortality was 92% (Holt et al. 1975). Mortality rates were 52, 92, and 99% at 17.8°C for juvenile spring Chinook, steelhead trout, and coho salmon respectively, and mortality dropped to 31, 56, and 51% at 15.0°C (Holt et al. 1975). At 12.2°C mortality varied from 4 to 20% among juveniles of the three species, and at temperatures of 9.4°C and below, no deaths due to the experimental infection with *F. columnaris* occurred (Holt et al. 1975). Holt et al. (1975) state that these results indicate that under the conditions of these experiments Columnaris disease was completely suppressed by water temperatures of 9.4°C or below.

In general, data from laboratory studies indicates that as water temperatures increase, the time to death decreases (Pacha et al. 1970). With juvenile steelhead trout and juvenile coho and spring Chinook salmon as the temperature increased above 12.2°C, the disease process was progressively accelerated, resulting in a minimum time to death at 20.5 or 23.3°C and a maximum at 12.2°C (Holt et al. 1975). In these juvenile salmonids Holt et al. (1975) found the mean time to death decreased from 7.6-12.2 days at 12.2°C to 1.6-1.7 days at 20.5°C for juvenile coho and steelhead, and 2.3 days at 23.3°C for juvenile spring Chinook (Holt et al. 1975).

1.8 TMDL Temperature Thresholds

Currently there are no numeric temperature standards in the *Water Quality Control Plan for the North Coast Region* (Basin Plan). Thus, information from this literature review will be utilized by Regional Water Board staff to selected chronic and acute temperature thresholds for evaluation of stream temperatures in TMDLs. Chronic temperature thresholds (MWMTs) were selected from the USEPA document *EPA Region 10 Guidance For Pacific Northwest State and Tribal Temperature Water Quality Standards* (2003), and are presented in Table 13. The Region 10 guidance is the product of a three-year interagency effort, and has been reviewed by both independent science review panels and the public. Acute lethal temperature thresholds were selected based upon best professional judgment of the literature, and are presented in Table 14.

Table 13: Life Stage Temperature Thresholds

Life Stage	MWMT (°C)
Adult Migration	20
Adult Migration plus Non-Core[1] Juvenile Rearing	18
Core[2] Juvenile Rearing	16
Spawning, Egg Incubation, and Fry Emergence	13

[1] Non-Core is defined as moderate to low density salmon and trout rearing usually occurring in the mid or lower part of the basin (moderate and low not defined).
[2] Core is defines as areas of high density rearing (high is not specifically defined).
Source: USEPA 2003

Table 14: Lethal Temperature Thresholds

Lethal Threshold[1] (°C)			
Life Stage	**Steelhead**	**Chinook**	**Coho**
Adult Migration and Holding	24	25	25
Juvenile Growth and Rearing	24	25	25
Spawning, Egg Incubation, and Fry Emergence	20	20	20

[1] The lethal thresholds selected in this table are generally for chronic exposure (greater than seven days). Although salmonids may survive brief periods at these temperatures, they are good benchmarks from the literature for lethal conditions.

In some cases it may be necessary to calculate MWATs for a given waterbody, and compare these to MWAT thresholds. USEPA (2003) states that for many rivers in the Pacific Northwest the MWMT is about 3°C higher than the MWAT (USEPA 2003, as cited by Dunham et al. 2001and Chapman 2002). Rather than list MWAT thresholds in this document using the 3°C difference suggested above, the Regional Water Board will consider stream temperatures within each individual TMDL waterbody. Thus the Regional Water Board will calculate both MWMTs and MWATs for the waterbody, and characterize the actual difference between these temperature metrics for the watershed using an approach similar to that used in Sullivan et al. (2000). Once this relationship is understood, MWAT thresholds for each life stage can be identified and compared to the watershed MWATs.

The freshwater temperature thresholds presented in this section are applicable during the season or time of year when the life stage of each species is present. Periodicity information is not discussed in this document and will be presented in each individual TMDL staff report. Where life history, timing, and/or species needs overlap, the lowest of each temperature metric applies.

CHAPTER 2. DISSOLVED OXYGEN and TOTAL DISSOLVED GAS

2.1 Introduction

Adequate concentrations of dissolved oxygen in fresh water streams are critical for the survival of salmonids. Fish have evolved very efficient physiological mechanisms for obtaining and using oxygen in the water to oxygenate the blood and meet their metabolic demands (WDOE 2002). Reduced levels of dissolved oxygen can impact growth and development of different life stages of salmon, including eggs, alevins, and fry, as well as the swimming, feeding and reproductive ability of juveniles and adults. Such impacts can affect fitness and survival by altering embryo incubation periods, decreasing the size of fry, increasing the likelihood of predation, and decreasing feeding activity. Under extreme conditions, low dissolved oxygen concentrations can be lethal to salmonids. High levels of total dissolved gas concentrations (TDG), including dissolved oxygen, can result in gas bubble disease and death for salmonids.

Literature reviewed for this analysis included EPA guidance, other states’ standards, reports that compiled and summarized existing scientific information, and numerous laboratory studies. When possible, species-specific requirements were summarized for the following life stages: migrating adults, incubation and emergence, and freshwater rearing and growth. The following information applies to salmonids in general, with specific references to coho, Chinook, steelhead, and other species of salmonids as appropriate.

2.2 Effects of Low Dissolved Oxygen Concentrations on Salmonids

2.2.1 Adult Migration

Reduced concentrations of dissolved oxygen can negatively affect the swimming performance of migrating salmonids (Bjornn and Reiser 1991). The upstream migration by adult salmonids is typically a stressful endeavor. Sustained swimming over long distances requires high expenditures of energy and therefore requires adequate levels of dissolved oxygen. Migrating adult Chinook salmon in the San Joaquin River exhibited an avoidance response when dissolved oxygen was below 4.2 mg/L, and most Chinook waited to migrate until dissolved oxygen levels were at 5 mg/L or higher (Hallock et al. 1970).

2.2.2 Incubation/Emergence

Low levels of dissolved oxygen can be directly lethal to salmonids, and can also have sublethal effects such as changing the rate of embryological development, the time to hatching, and size of emerging fry (Spence et al. 1996). The embryonic and larval stages of salmonid development are especially susceptible to low dissolved oxygen levels as their ability to extract oxygen is not fully developed and their relative immobility inhibits their ability to migrate to more favorable conditions. The dissolved oxygen requirements for successful incubation of embryos and emergence of fry is tied to intragravel dissolved oxygen levels. Intragravel dissolved oxygen is typically a function of many chemical, physical, and hydrological variables, including: the dissolved oxygen concentration of the overlying stream water, water temperature, substrate size and porosity, biochemical oxygen demand of the intragravel water, sediment oxygen demand, the gradient and velocity of the stream, channel configuration, and depth of water. As a result the dissolved oxygen concentration within the gravels can be depleted causing problems for salmonid embryos and larvae, even when overlying surface water oxygen levels are suitable (USEPA 1986a).

Studies note that water column dissolved oxygen concentrations are typically estimated to be reduced by 1-3 mg/L as water is transmitted to redds containing developing eggs and larvae (WDOE 2002). USEPA (1986a) concluded that dissolved oxygen levels within the gravels should be considered to be at least 3 mg/L lower than concentrations in the overlying water. ODEQ (1995b) expect the loss of an average of 3 mg/L dissolved oxygen from surface water to the gravels.

2.2.3 Incubation Mortality

Phillips and Campbell (1961, as cited by Bjornn and Reiser 1991) concluded that intragravel dissolved oxygen must average 8 mg/L for embryos and alevins to survive well. After reviewing numerous studies Davis (1975) states that a dissolved oxygen concentration of 9.75 mg/L is fully protective of larvae and mature eggs, while at 8 mg/L the average member of the incubating population will exhibit symptoms of oxygen distress, and at 6.5 mg/L a large portion of the incubating eggs may be affected. Bjornn and Reiser (1991) reviewed numerous references and recommend that dissolved oxygen should drop no lower than 5 mg/L, and should be at or near saturation for successful incubation.

In a review of several laboratory studies, ODEQ (1995b) concluded that at near optimum (10°C) constant temperatures acute mortality to salmonid embryos occurs at relatively low concentrations of dissolved oxygen, near or below 3 mg/L. Field studies reviewed by ODEQ (1995b) demonstrate that embryo survival is low when the dissolved oxygen content in the gravels drops near or below 5 mg/L, and survival is greater at 8 mg/L.

Silver et al. (1963) performed a study with Chinook salmon and steelhead trout, rearing eggs at various constant dissolved oxygen concentrations and water velocities. They found that steelhead embryos held at 9.5°C and Chinook salmon embryos held at 11°C experienced complete mortality at dissolved oxygen concentrations of 1.6 mg/L. Survival of a large percentage of embryos reared at oxygen levels as low as 2.5 mg/L appeared to be possible by reduction of respiration rates and consequent reduction of growth and development rates.

In a field study Cobel (1961) found that the survival of steelhead embryos was correlated to intragravel dissolved oxygen in the redds, with higher survival at higher levels of dissolved oxygen. At 9.25 mg/L survival was 62%, but survival was only 16% at 2.6 mg/L. A laboratory study by Eddy (1971) found that Chinook salmon survival at 10.4 mg/L (13.5 °C) was approximately 67%, however at dissolved oxygen levels of 7.3 mg/L (13.5 °C) survival dropped to 49-57.6%. At temperatures more suitable for Chinook incubation (10.5 °C) Eddy (1971) found the percent survival remained high (over 90%) at dissolved oxygen levels from 11 mg/L to 3.5 mg/L; however, as dissolved oxygen levels decreased, the number of days to hatching increased and the mean dry weight of the fry decreased substantially. WDOE (2002) also points out that the studies above did not consider the act of emerging through the redds, and the metabolic requirements to emerge would be expected to be substantial. Therefore, it is likely that higher oxygen levels may be needed to fully protect hatching and emergence, than to just support hatching alone.

2.2.4 Incubation Growth

Embryos can survive when dissolved oxygen is below saturation (and above a critical level), but development typically deviates from normal (Bjornn and Reiser 1991). Embryos were found to be smaller than normal, and hatching either delayed or premature, when dissolved oxygen was below saturation throughout development (Doudoroff and Warren 1965, as cited by Bjornn and Reiser 1991).

Garside (1966) found the number of days it took for rainbow trout to go from fertilization to hatching increased as dissolved oxygen concentrations and water temperature decreased. In this study, rainbow trout were incubated at temperatures between 2.5 - 17.5°C and dissolved oxygen levels from 2.5 - 11.3 mg/L. At 10°C and 7.5°C the total time for incubation was delayed 6 and 9 days respectively at dissolved oxygen levels of 2.5 mg/L versus embryos incubated at approximately 10.5 mg/L.

Silver et al. (1963) found that hatching of steelhead trout held at 9.5°C was delayed 5 to 8 days at dissolved oxygen concentrations averaging 2.6 mg/L versus embryos reared at 11.2 mg/L. A smaller delay of hatching was observed at oxygen levels of 4.2 and 5.7 mg/L, although none was apparent at 7.9 mg/L. For Chinook salmon held at 11°C, Silver et al. observed that embryos reared at oxygen levels lower than 11 mg/L experienced a delay in hatching, with the most significant delay in those reared at dissolved oxygen levels of 2.5 mg/L (6 to 9 days). The size of both Chinook and steelhead embryos increased with increases in dissolved oxygen up to 11.2 mg/L. External examination of embryos revealed abnormal structural development in Chinook salmon tested at dissolved oxygen concentrations of 1.6 mg/L, and abnormalities in steelhead trout at concentrations of 1.6 and 2.6 mg/L. The survival of Chinook salmon after hatching was only depressed at the 2.5 mg/L level, the lowest level at which hatching occurred, with lower mortalities occurring at higher velocities. Post hatching survival of steelhead trout could not be determined due to numerous confounding factors.

Shumway et al. (1964) conducted a laboratory study to determine the influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. The experiments were conducted at a temperature of 10°C and oxygen levels generally ranging from 2.5 - 11.5 mg/L and flows from 3 to 750 cm/hour. It was concluded that the median time to hatching decreased and size of fry increased as dissolved oxygen levels increased. For example, steelhead trout embryos reared at 2.9 mg/L hatched in approximately 41 days and had a wet weight of 17 mg, while embryos reared at 11.9 mg/L hatched in 36 days and weighed 32.3 mg. The authors found that a reduction of either the oxygen concentration or the water velocity will reduce the size of fry and increase the incubation period, although the affect of various water velocities tested was less than the effect of the different dissolved oxygen concentrations tested.

WDOE (2002) reviewed various references and found that at favorable incubation temperatures a mean oxygen concentration of 10.5 mg/L will result in a 2% reduction in growth. At other oxygen concentrations, growth is reduced as follows: 8% reduction at oxygen levels of 9 mg/L, 10% reduction at 7 mg/L, and a 25% reduction at 6 mg/L.

2.2.5 Incubation Avoidance/Preference

Alevin showed a strong preference for oxygen concentrations of 8 - 10 mg/L and moved through the gravel medium to these concentrations, avoiding concentrations from 4 - 6 mg/L (WDOE 2002).

2.2.6 Emergence Mortality

"The hatching time, size, and growth rate of developing embryos is proportional to the dissolved oxygen concentrations up to 8 mg/L or greater. The ability of fry to survive their natural environment may be related to the size of fry at hatch (ODEQ 1995b)." McMahon (1983) recommends dissolved oxygen levels be ≥ 8 mg/L for high survival and emergence of fry. In a review of controlled field and lab studies on emergence, WDOE (2002) states that average intragravel oxygen concentrations of 6 - 6.5 mg/L and lower can cause stress and mortality in developing embryos and alevin. It is also noted that field studies on emergence consistently cite intragravel oxygen concentrations of 8 mg/L or greater as being associated with or necessary for superior health and survival, oxygen concentrations below 6 - 7 mg/L result in a 50% reduction in survival through emergence, and oxygen concentrations below 5 mg/L result in negligible survival. According to various laboratory studies, the threshold for complete mortality of emerging salmonids is noted to occur between 2 - 2.5 mg/L (WDOE 2002).

After reviewing numerous literature sources, the USEPA (1986a) concluded that the embryonic and larval stages of salmonid development will experience no impairment when water column dissolved oxygen concentrations are 11 mg/L. This translates into an intragravel dissolved oxygen concentration of 8 mg/L (USEPA assumes a 3 mg/L loss between the surface water and gravels). Table 15 from the USEPA (1986a) lists the water column and intragravel dissolved oxygen concentrations associated with various health effects. These health affects range from no production impairment to acute mortality.

Table 15: Dissolved oxygen concentrations and their effects salmonid embryo and larval stages

Level of Effect	**Water Column DO (mg/L)**	**Intragravel DO (mg/L)**
No Production Impairment	11	8*
Slight Production Impairment	9	6*
Moderate Production Impairment	8	5*
Severe Production Impairment	7	4*
Limit to Avoid Acute Mortality	6	3*

* A 3 mg/L loss is assumed between the water column dissolved oxygen levels and those intragravel.
Source: USEPA 1986a

2.2.7 Freshwater Rearing and Growth

2.2.7.1 Swimming and Activity

Salmonids are strong active swimmers requiring highly oxygenated waters (Spence 1996), and this is true during the rearing period when the fish are feeding, growing, and avoiding predation. Salmonids may be able to survive when dissolved oxygen concentrations are low (<5 mg/L), but growth, food conversion efficiency, and swimming performance will be adversely affected (Bjornn and Reiser 1991). Davis (1975) reviewed numerous studies and reported no impairment to rearing salmonids if dissolved oxygen concentrations averaged 9 mg/L, while at oxygen levels of 6.5 mg/L "the average member of the community will exhibit symptoms of oxygen distress", and at 4 mg/L a large portion of salmonids may be affected. Dahlberg et al. (1968) state that at temperatures near 20°C any considerable decrease in the oxygen concentration below 9 mg/L (the air saturation level) resulted in some reduction of the final swimming speed. They found that between dissolved oxygen concentrations of 7 to 2 mg/L the swimming speed of coho declined markedly with the decrease in dissolved oxygen concentration.

In a laboratory study, Davis et al. (1963) reported that the maximum sustainable swimming speeds of wild juvenile coho salmon were reduced when dissolved oxygen dropped below saturation at water temperatures of 10, 15, and 20°C. Air-saturation values for these dissolved oxygen concentrations were cited as 11.3, 10.2, and 9.2 mg/L respectively. They found that the maximum sustained swimming speeds (based on first and second swimming failures at all temperatures) were reduced by 3.2 - 6.4%, 5.9 - 10.1%, 9.9 - 13.9%, 16.7 - 21.2%, and 26.6 - 33.8% at dissolved oxygen concentrations of 7, 6, 5, 4, and 3 mg/L respectively. The authors also conducted tests on juvenile Chinook salmon and found that the percent reductions from maximum swimming speed at temperatures ranging from 11 to 15°C were greater than those for juvenile coho. At the dissolved oxygen concentrations listed above swimming speeds were decreased by 10%, 14%, 20%, 27%, and 38% respectively.

WDOE (2002) reviewed various data and concluded that swimming fitness of salmonids is maximized when the daily minimum dissolved oxygen levels are above 8 - 9 mg/L. Jones et al. (1971, as cited by USEPA 1986a) found the swimming speed of rainbow trout was decreased 30% from maximum at dissolved oxygen concentrations of 5.1 mg/L and 14°C. At oxygen levels of 3.8 mg/L and a temperature of 22°C, they found a 43% reduction in the maximum swimming speed.

2.2.7.2 Growth

In a review of constant oxygen exposure studies WDOE (2002) concluded salmonid growth rates decreased less than 10% at dissolved oxygen concentrations of 8 mg/L or more, less than 20% at 7 mg/L, and generally less than 22% at 5 - 6 mg/L. Herrmann (1958) found that the mean percentage of weight gain in juvenile coho held at constant dissolved oxygen concentrations was 7.2% around 2 mg/L, 33.6% at 3 mg/L, 55.8% near 4 mg/L, and 67.9% at or near 5 mg/L. In a laboratory study Fischer (1963) found that the growth rates of juvenile coho exposed to constant oxygen concentrations ranging from 2.5 to 35.5 mg/L (fed to satiation, temperature at approximately 18 °C) dramatically decreased with decreases in the oxygen concentration below 9.5 mg/L (air saturation level). WDOE (2002) concludes that a monthly or weekly average concentration of 9 mg/L, and a monthly average of the daily minimum concentrations should be at or above 8 - 8.5 mg/L to have a negligible effect (5% or less) on growth and support healthy growth rates.

Food conversion efficiency is related to dissolved oxygen levels and the process becomes less efficient when oxygen concentrations are below 4 - 4.5 mg/L (ODEQ 1995b). Bjornn and Reiser (1991) state that growth, food conversion efficiency, and swimming performance are adversely affected when dissolved oxygen concentrations are <5 mg/L. The USEPA (1986a) reviewed growth data from a study conducted by Warren et al. (1973) where tests were conducted at various temperatures to determine the growth of coho and Chinook. USEPA cites that, with the exception of tests conducted at 22 °C, the results supported the idea that the effects of low dissolved oxygen become more severe at higher temperatures.

Brett and Blackburn (1981) performed a laboratory study to determine the growth rate and food conversion efficiency of young coho and sockeye salmon fed full rations. Tests were performed at dissolved oxygen concentrations ranging from 2 to 15 mg/L at a constant temperature of 15°C, the approximate optimum temperature for growth of Pacific Salmon. Both species showed a strong dependence of growth on the environmental oxygen concentrations when levels were below 5 mg/L. For coho, zero growth was observed at dissolved oxygen concentrations of 2.3 mg/L. The mean value for maximum coho growth occurred at 4 mg/L, and at dissolved oxygen concentrations above this level growth did not appear to be dependant on the dissolved oxygen. Sockeye displayed zero growth at oxygen levels of 2.6 mg/L, and reached the zone of independence (growth not dependant on dissolved oxygen levels) at 4.2 mg/L. Brett and Blackburn (1981) conclude that the critical inflection from oxygen dependence to independence occurs at 4 - 4.2 mg/L for coho and sockeye.

Herrmann et al. (1962) studied the influence of various oxygen concentrations on the growth of age 0 coho salmon held at 20 °C. Coho were held in containers at a constant mean dissolved oxygen level ranging from 2.1 - 9.9 mg/L and were fed full rations. The authors concluded that oxygen concentrations below 5 mg/L resulted in a sharp decrease in growth and food consumption. A reduction in the mean oxygen levels from 8.3 mg/L to 6 and 5 mg/L resulted in slight decreases in food consumption and growth. Weight gain in grams per gram of food consumed was slightly depressed at dissolved oxygen concentrations near 4 mg/L, and were markedly reduced at lower concentrations. At oxygen levels of 2.1 and 2.3 mg/L, many fish died and the surviving fish lost weight and consumed very little food.

USEPA (1986a) calculated the median percent reduction in growth rate of Chinook and coho salmon fed full rations at various dissolved oxygen concentrations. They calculated no reduction in growth at dissolved oxygen concentrations of 8 and 9 mg/L, and a 1% reduction in growth at 7 mg/L for both species. At 6 mg/L Chinook and coho growth were reduced by 7% and 4% respectively. Dissolved oxygen levels of 4 mg/L result in a

29% reduction in growth for Chinook salmon and 21% reduction in growth for coho. At 3 mg/L there was a 47% decrease in Chinook growth and a 37% reduction in coho growth. USEPA (1986a) states that due to the variability inherent in growth studies the reductions in growth rates seen above 6 mg/L are not usually statistically significant, while reductions in growth at dissolved oxygen levels below 4 mg/L are considered severe.

2.2.7.3 Avoidance and Preference

Salmonids have been reported to actively avoid areas with low dissolved oxygen concentrations, which is likely a useful protective mechanism that enhances survival (Davis 1975). Field and laboratory studies have found that avoidance reactions in juvenile salmonids consistently occur at concentrations of 5 mg/L and lower, and there is some indication that avoidance is triggered at concentrations as high as 6 mg/L. Therefore these dissolved oxygen levels should be considered a potential barrier to the movement and habitat selection of salmonids (WDOE 2002).

Spoor (1990) performed a laboratory study on the distribution of fingerling brook trout in dissolved oxygen concentration gradients. Sixteen gradients between 1 and 8.9 mg/L were used for the study to determine what level of dissolved oxygen is preferred by the brook trout. It was found that in the absence of a gradient with dissolved oxygen concentrations at 6 mg/L or more throughout the system, the fish moved freely without showing preference or avoidance. Movement from low to higher oxygen concentrations were noted throughout the study. Fish moved away from water with dissolved oxygen concentrations from 1 - 1.9 mg/L within one hour, moved away from water with dissolved oxygen concentrations of 2 - 2.9 mg/L within 1 - 2 hours, and moved away more slowly from concentrations of 3 - 3.9 mg/L. From his study, Spoor (1990) concluded that brook trout will avoid oxygen concentrations below 4 mg/L, and preferred oxygen levels of 5 mg/L or higher.

Whitmore et al. (1960) performed studies with juvenile coho and Chinook salmon to determine their avoidance reaction to dissolved oxygen concentration of 1.5, 3 , 4.5, and 6 mg/L at variable river water temperatures. Juvenile Chinook salmon showed marked avoidance of oxygen concentrations near 1.5, 3, and 4.5 mg/L in the summer at mean temperatures ranging from 20.7 - 22.8°C, but no avoidance to levels near 6 mg/L at a mean temperature of 18.4°C. Chinook did not show as strong an avoidance to these oxygen levels in the fall when water temperatures were lower, ranging from 11.8 - 13.2°C. Chinook showed little avoidance of dissolved oxygen concentrations near 4.5 mg/L during the fall, and no avoidance to concentrations near 6 mg/L. In all cases avoidance became progressively larger with reductions in the oxygen concentration below 6 mg/L. Seasonal differences of avoidance are most likely due to differences in water temperature. At temperatures ranging from 18.4 - 19°C juvenile coho salmon showed some avoidance to all of the above oxygen concentrations, including 6 mg/L. Their behavior was more erratic than that of Chinook, and their avoidance of concentrations near 4.5 mg/L and lower was not as pronounced at corresponding temperatures. The juvenile coho often started upon entering water with low dissolved oxygen and then darted around until they found their way out of the experimental channel.

USEPA (1986a) performed a literature review and cites the effects of various dissolved oxygen concentrations on salmonid life stages other than embryonic and larval (Table 16). These effects range from no impairment at 8 mg/L to acute mortality at dissolved oxygen levels below 3 mg/L.

Table 16: Dissolved oxygen concentrations and their effects on salmonid life stages other than embryonic and larval

Level of Effect	**Water Column DO (mg/L)**
No Production Impairment	8
Slight Production Impairment	6
Moderate Production Impairment	5
Severe Production Impairment	4
Limit to Avoid Acute Mortality	3

Source: USEPA 1986a

2.2.8 Lethality

Salmonid mortality begins to occur when dissolved oxygen concentrations are below 3 mg/L for periods longer than 3.5 days (USEPA 1986a). A summary of various field study results by WDOE (2002) reports that significant mortality occurs in natural waters when dissolved oxygen concentrations fluctuate the range of 2.5 - 3 mg/L. Long-term (20 - 30 days) constant exposure to mean dissolved oxygen concentrations below 3 - 3.3 mg/L is likely to result in 50% mortality of juvenile salmonids (WDOE 2002). According to a short-term (1 - 4 hours) exposure study by Burdick et al. (1954, as cited by WDOE, 2002), in warm water (20 - 21°C) salmonids may require daily minimum oxygen levels to remain above 2.6 mg/L to avoid significant (50%) mortality. From these and other types of studies, WDOE (2002) concluded that juvenile salmonid mortality can be avoided if daily minimum dissolved oxygen concentration remain above 3.9 mg/L, and the monthly or weekly average of minimum concentrations remains above 4.6 mg/L.

2.3 Effects of High Total Dissolved Gas Concentrations on Salmonids

High levels of total dissolved gas (TDG), including dissolved oxygen, can be harmful to salmonids and other fish and result in “gas bubble disease”. This occurs when dissolved gases in their circulatory system come out of solution and form bubbles which block the flow of blood through the capillary vessels (USEPA 1986b). There are several ways TDG supersaturation can occur, including excessive algal photosynthesis which can create supersaturated dissolved oxygen conditions (USEPA 1986b). Thus, to protect salmonids and other freshwater fish the USEPA has set criteria for TDG stating that levels should not exceed 110% of the saturation value.

Numerous studies have been conducted to determine the mortality rate of salmonids exposed to various levels of TDG. Mesa et al. (2000) conducted laboratory experiments on juvenile Chinook and steelhead, exposing them to different levels of TDG and found no fish died when held at 110% TDG for up to 22 days. When fish were exposed to 120% TDG, 20% of juvenile Chinook died within 40 to 120 hours while 20% of juvenile steelhead died within 20 to 35 hours. At TDG levels of 130% Chinook mortality reached 20% after 3 to 6 hours and steelhead mortality was 20% after 5 to 7 hours. Gale et al. (2001) held adult female spring Chinook at mean TDG levels ranging from 114.1% to 125.5% and found the time to first mortality ranged from 10 to 68 hours.

USEPA (1986b) discusses various studies on the effects of TDG on salmonids. The following studies are all cited from the USEPA 1986 water quality criteria document. Bouck et al. (1975) found TDG levels of 115% and above to be acutely lethal to most species of salmonids, and levels of 120% TDG are rapidly lethal to all salmonids. Conclusions drawn from Ebel et al. (1975) and Rulfison and Abel (1971) include the following:

- Adult and juvenile salmonids confined to shallow water (1 m) with TDG levels above 115% experience substantial levels of mortality.
- Juvenile salmonids exposed sublethal levels TDG supersaturation are able to recover when returned to normally saturated water, while adults do not recover and generally die.

CHAPTER 3. AMMONIA

3.1 Introduction

According to the USEPA (1986b, p.17), acute concentrations of ammonia can cause loss of equilibrium, hyperexcitability, increased breathing, cardiac output and oxygen uptake, and, in extreme cases, convulsions, coma, and death of fish. Lower concentrations of ammonia can result in reduced hatching success, reduced growth and morphological development, and pathologic changes in tissues of gills, livers, and kidneys.

The information in the following sections was extracted from the USEPA document titled: *1999 Update of Ambient Water Quality Criteria for Ammonia*. The information presented applies to salmonids in general.

3.2 Ammonia Speciation

Ammonia in water exists primarily in two forms, un-ionized ammonia (NH_3) and ammonium ion (NH_4^+) (USEPA 1999b, p.2). The fraction of each of these two forms, or ammonia speciation, varies markedly with temperature and pH (USEPA 1999b, p.2). The pH-dependence of the relative amounts of un-ionized ammonia and ammonium ion at 25°C are presented in Figure 1 below (USEPA 1999b, p.2). Ammonia speciation also depends on ionic strength, although in freshwater this effect is much smaller than the effects of temperature and pH (USEPA 1999b, p.3)

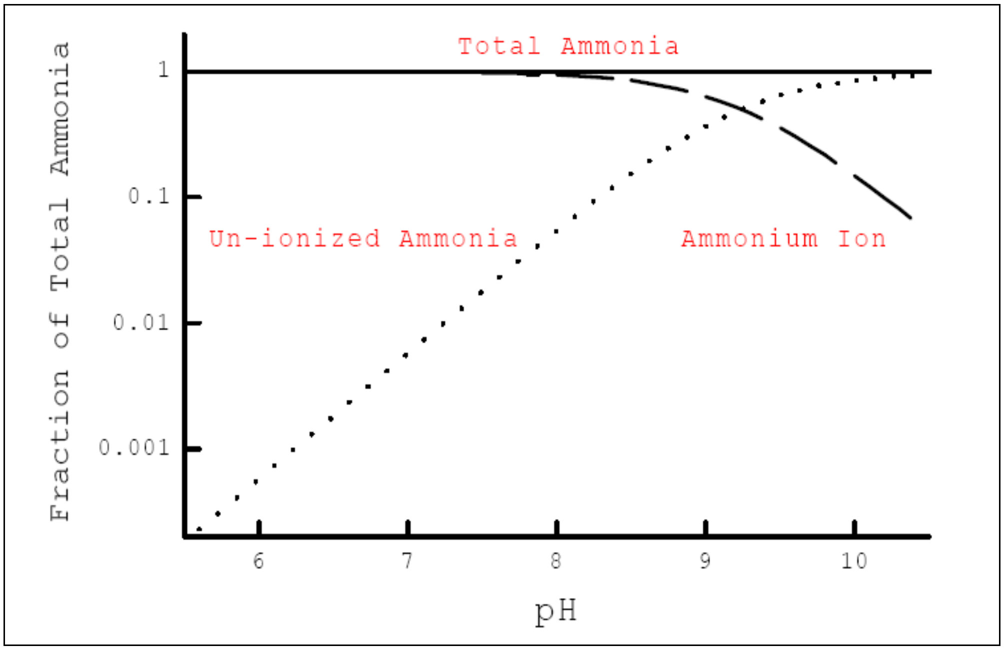


Figure 1: Chemical Speciation of Ammonia
Source: USEPA 1999b, p.3

3.3 Ammonia Toxicity

> These speciation relationships are important to ammonia toxicity because un-ionized ammonia is much more toxic than ammonium ion. The importance of un-ionized ammonia was first recognized when it was observed that increased pH caused total ammonia to appear to be much more toxic (Chipman 1934; Wuhrmann and Woker 1948). It is not surprising that un-ionized ammonia is the more toxic form, because it is a neutral molecule and thus is able to diffuse across the epithelial membranes of aquatic organisms much more readily than the charged ammonium ion. Ammonia is unique among regulated pollutants because it is an endogenously produced toxicant that organisms have developed various strategies to excrete, which is in large part by passive diffusion of un-ionized ammonia from the gills. High external un-ionized ammonia concentrations reduce or reverse diffusive gradients and cause the buildup of ammonia in gill tissue and blood (USEPA 1999b, p.3).
>
> Because of the importance of un-ionized ammonia, it became a convention in the scientific literature to express ammonia toxicity in terms of un-ionized ammonia, and water quality criteria and standards followed this convention. However, there are reasons to believe that ammonium ion can contribute significantly to ammonia toxicity under some conditions. Observations that ammonia toxicity is relatively constant when expressed in terms of un-ionized ammonia come mainly from toxicity tests conducted at pH>7.5. At lower pH, toxicity varies considerably when expressed in terms of unionized ammonia and under some conditions is relatively constant in terms of ammonium ion (Erickson 1985). Also, studies have established that mechanisms exist for the transport of ammonium ion across gill epithelia (Wood 1993), so this ion might contribute significantly to ammonia exchange at gills and affect the buildup of ammonia in tissues if its external concentration is sufficiently high. Thus, the very same arguments employed for the importance of un-ionized ammonia can also be applied in some degree to ammonium ion. This is not to say that ammonium ion is as toxic as unionized ammonia, but rather that, regardless of its lower toxicity, it can still be important because it is generally present in much greater concentrations than un-ionized ammonia (USEPA 1999b, p.3,4).

3.4 Ammonia Criteria

The USEPA has utilized the above information to create pH-dependant acute and pH- and temperature-dependent chronic criterion for total ammonia (NH_3 and NH_4^+) as nitrogen in freshwater (Tables 17, 18, 19).

Table 17: pH-Dependent Values of the Criterion Maximum Concentration (CMC) of Total Ammonia as Nitrogen (mg N/L) in Freshwater when Salmonids are Present

Acute Criterion[1]

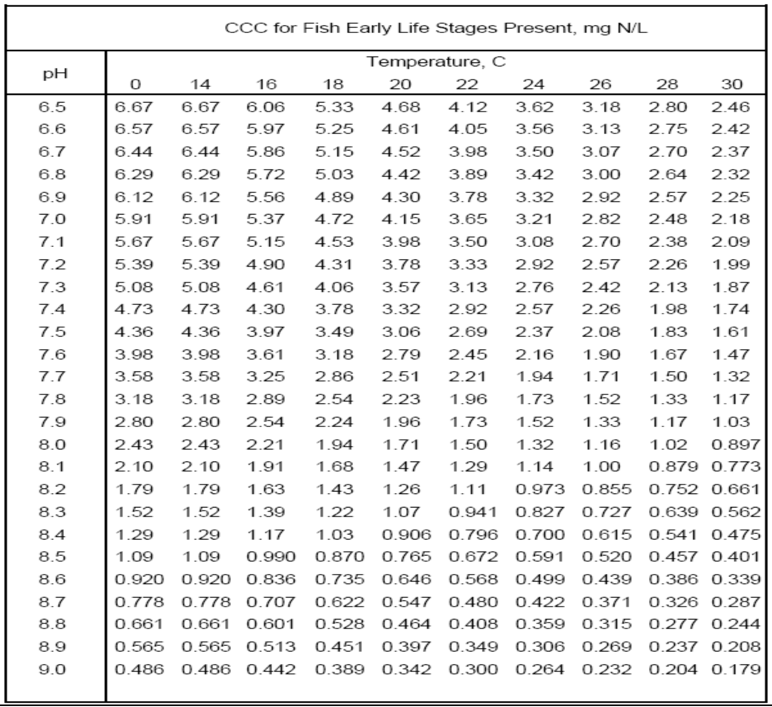
pH	CMC Total NH3 mgN/L	pH	CMC Total NH3 mgN/L
6.5	32.6	7.8	8.11
6.6	31.3	7.9	6.77
6.7	29.8	8.0	5.62
6.8	28.1	8.1	4.64
6.9	26.2	8.2	3.83
7.0	24.1	8.3	3.15
7.1	22.0	8.4	2.59
7.2	19.7	8.5	2.14
7.3	17.5	8.6	1.77
7.4	15.4	8.7	1.47
7.5	13.3	8.8	1.23
7.6	11.4	8.9	1.04
7.7	9.65	9.0	0.885

[1] The one-hour average concentration of total ammonia nitrogen (NH_3 and NH_4^+) should not exceed this value more than once every 3 years.

Source: USEPA 1999b, p.86

Table 18: Temperature and pH-Dependent Values of the Criterion Continuous Continuation (CCC) for Total Ammonia as Nitrogen (mg N/L) in Freshwater when Fish Early Life Stages are Present

Chronic Criterion[1]



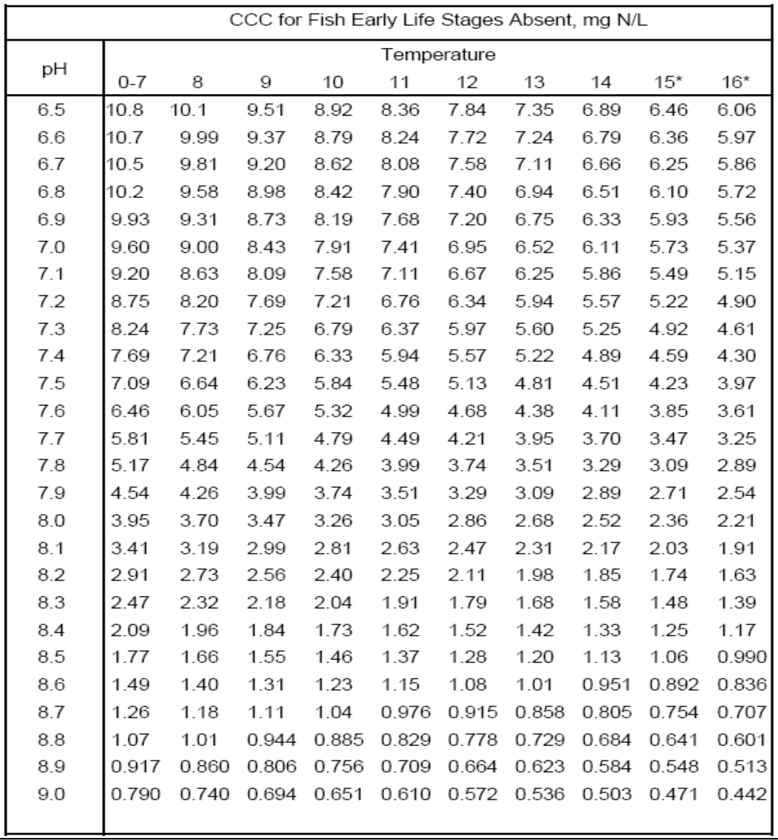
CCC for Fish Early Life Stages Present, mg N/L

pH	Temperature, C									
	0	14	16	18	20	22	24	26	28	30
6.5	6.67	6.67	6.06	5.33	4.68	4.12	3.62	3.18	2.80	2.46
6.6	6.57	6.57	5.97	5.25	4.61	4.05	3.56	3.13	2.75	2.42
6.7	6.44	6.44	5.86	5.15	4.52	3.98	3.50	3.07	2.70	2.37
6.8	6.29	6.29	5.72	5.03	4.42	3.89	3.42	3.00	2.64	2.32
6.9	6.12	6.12	5.56	4.89	4.30	3.78	3.32	2.92	2.57	2.25
7.0	5.91	5.91	5.37	4.72	4.15	3.65	3.21	2.82	2.48	2.18
7.1	5.67	5.67	5.15	4.53	3.98	3.50	3.08	2.70	2.38	2.09
7.2	5.39	5.39	4.90	4.31	3.78	3.33	2.92	2.57	2.26	1.99
7.3	5.08	5.08	4.61	4.06	3.57	3.13	2.76	2.42	2.13	1.87
7.4	4.73	4.73	4.30	3.78	3.32	2.92	2.57	2.26	1.98	1.74
7.5	4.36	4.36	3.97	3.49	3.06	2.69	2.37	2.08	1.83	1.61
7.6	3.98	3.98	3.61	3.18	2.79	2.45	2.16	1.90	1.67	1.47
7.7	3.58	3.58	3.25	2.86	2.51	2.21	1.94	1.71	1.50	1.32
7.8	3.18	3.18	2.89	2.54	2.23	1.96	1.73	1.52	1.33	1.17
7.9	2.80	2.80	2.54	2.24	1.96	1.73	1.52	1.33	1.17	1.03
8.0	2.43	2.43	2.21	1.94	1.71	1.50	1.32	1.16	1.02	0.897
8.1	2.10	2.10	1.91	1.68	1.47	1.29	1.14	1.00	0.879	0.773
8.2	1.79	1.79	1.63	1.43	1.26	1.11	0.973	0.855	0.752	0.661
8.3	1.52	1.52	1.39	1.22	1.07	0.941	0.827	0.727	0.639	0.562
8.4	1.29	1.29	1.17	1.03	0.906	0.796	0.700	0.615	0.541	0.475
8.5	1.09	1.09	0.990	0.870	0.765	0.672	0.591	0.520	0.457	0.401
8.6	0.920	0.920	0.836	0.735	0.646	0.568	0.499	0.439	0.386	0.339
8.7	0.778	0.778	0.707	0.622	0.547	0.480	0.422	0.371	0.326	0.287
8.8	0.661	0.661	0.601	0.528	0.464	0.408	0.359	0.315	0.277	0.244
8.9	0.565	0.565	0.513	0.451	0.397	0.349	0.306	0.269	0.237	0.208
9.0	0.486	0.486	0.442	0.389	0.342	0.300	0.264	0.232	0.204	0.179

[1] The thirty-day average concentration of total ammonia (NH_3 and NH_4^+) should not exceed this value more than once every three years. Additionally, the highest four day average within the thirty-day period should not exceed 2.5 times the CCC (USEPA 1999b, p.87).

Table 19: Temperature and pH-Dependent Values of the Criterion Continuous Continuation (CCC) for Total Ammonia as Nitrogen (mg N/L) in Freshwater when Fish Early Life Stages are Absent

Chronic Criterion[1]



CCC for Fish Early Life Stages Absent, mg N/L

pH	Temperature									
	0-7	8	9	10	11	12	13	14	15*	16*
6.5	10.8	10.1	9.51	8.92	8.36	7.84	7.35	6.89	6.46	6.06
6.6	10.7	9.99	9.37	8.79	8.24	7.72	7.24	6.79	6.36	5.97
6.7	10.5	9.81	9.20	8.62	8.08	7.58	7.11	6.66	6.25	5.86
6.8	10.2	9.58	8.98	8.42	7.90	7.40	6.94	6.51	6.10	5.72
6.9	9.93	9.31	8.73	8.19	7.68	7.20	6.75	6.33	5.93	5.56
7.0	9.60	9.00	8.43	7.91	7.41	6.95	6.52	6.11	5.73	5.37
7.1	9.20	8.63	8.09	7.58	7.11	6.67	6.25	5.86	5.49	5.15
7.2	8.75	8.20	7.69	7.21	6.76	6.34	5.94	5.57	5.22	4.90
7.3	8.24	7.73	7.25	6.79	6.37	5.97	5.60	5.25	4.92	4.61
7.4	7.69	7.21	6.76	6.33	5.94	5.57	5.22	4.89	4.59	4.30
7.5	7.09	6.64	6.23	5.84	5.48	5.13	4.81	4.51	4.23	3.97
7.6	6.46	6.05	5.67	5.32	4.99	4.68	4.38	4.11	3.85	3.61
7.7	5.81	5.45	5.11	4.79	4.49	4.21	3.95	3.70	3.47	3.25
7.8	5.17	4.84	4.54	4.26	3.99	3.74	3.51	3.29	3.09	2.89
7.9	4.54	4.26	3.99	3.74	3.51	3.29	3.09	2.89	2.71	2.54
8.0	3.95	3.70	3.47	3.26	3.05	2.86	2.68	2.52	2.36	2.21
8.1	3.41	3.19	2.99	2.81	2.63	2.47	2.31	2.17	2.03	1.91
8.2	2.91	2.73	2.56	2.40	2.25	2.11	1.98	1.85	1.74	1.63
8.3	2.47	2.32	2.18	2.04	1.91	1.79	1.68	1.58	1.48	1.39
8.4	2.09	1.96	1.84	1.73	1.62	1.52	1.42	1.33	1.25	1.17
8.5	1.77	1.66	1.55	1.46	1.37	1.28	1.20	1.13	1.06	0.990
8.6	1.49	1.40	1.31	1.23	1.15	1.08	1.01	0.951	0.892	0.836
8.7	1.26	1.18	1.11	1.04	0.976	0.915	0.858	0.805	0.754	0.707
8.8	1.07	1.01	0.944	0.885	0.829	0.778	0.729	0.684	0.641	0.601
8.9	0.917	0.860	0.806	0.756	0.709	0.664	0.623	0.584	0.548	0.513
9.0	0.790	0.740	0.694	0.651	0.610	0.572	0.536	0.503	0.471	0.442

[1] The thirty-day average concentration of total ammonia (NH_3 and NH_4^+) should not exceed this value more than once every three years. Additionally, the highest four day average within the thirty-day period should not exceed 2.5 times the CCC.

Source: USEPA 1999b, p.88

CHAPTER 4. pH

4.1 Introduction

The pH of freshwater streams is important for adult and juvenile salmonid development. Chronic effects from low pH can occur at levels that are not toxic to adult fish but that impair reproduction including altered spawning behavior, reduced egg viability, decreased hatchability, and reduced survival of the early life stages (Jordahl and Benson 1987). The early life stages of salmonid development are most vulnerable to low pH (Jordahl and Benson 1987). Chronic high pH levels in freshwater streams can decrease activity levels of salmonids, create stress responses, decrease or cease feeding, and lead to a loss of equilibrium (Murray and Ziebell 1984; Wagner et al. 1997). Additionally, high temperatures can exacerbate the effects of high pH levels on salmonids (Wagner et al. 1997). If pH reaches extremely low or high levels, death can occur (Wagner et al. 1997).

Literature reviewed for this analysis included numerous laboratory and field studies. The following information applies to salmonids in general.

4.2 Effects of High pH

Wagner et al. (1997) conducted laboratory and field studies and found that pH values of greater than 9.4 will result in the death of rainbow trout, especially at temperatures ranging from 19-22 C. Fresh water pH values of 9.0 or greater resulted in significant stress responses in rainbow trout.

Wilkie and Wood (1996) found that Lahontan cutthroat trout exposed to high pH waters (9.4) permanently lowered their rate of nitrogenous waste production to avoid the potentially toxic build-up of internal ammonia. However, rainbow trout, kokanee, and brown trout were unable to adapt to the high pH and died.

Murray and Ziebell (1984) found that rainbow trout are not able to acclimate to pH levels of 10.0 or higher and that their ability to tolerate pH above 9.0 depends on the rate of acclimation. Gradual acclimation (0.2 to 0.4 of a pH unit/day) allowed rainbow trout to acclimate to a pH of 9.8 and continue feeding, although they showed signs of distress and their activity was greatly reduced by the end of 4 days when the pH reached 9.9 (Table 20). The maximum pH tolerated before fish began dying was 10.2.

Rapid acclimations tests conducted by Murray and Ziebell (1984) yeilded the following results:

> Rainbow trout mortalities were 40% or greater in preliminary acclimation tests in which pH was increased to 9.6 and 9.7 in 3 and 5 hours. These results were comparable to previous shock tests (unpublished data). Consequently, in later experiments, acclimation time was increased to 6 hours and pH values were lowered to 9.3 and 9.5.

Trout in the pH 9.5 experiments exhibited adverse reactions and mortalities were similar to those seen in preliminary tests at pH 9.6 and 9.7. All fish began to show marked signs of stress within 12 hours, and within 24 hours the mortalities in replicated experiments were 30, 40, and 50% respectively. At 49 hours the last deaths occurred that brought mortalities to 50% in each replicate. All remaining living fish were distressed and did not feed. After 72 hours had elapsed, the survivors resumed feeding and their condition improved until the experiments were terminated at 120 hours.

In the pH 9.3, 6-hour acclimation experiments trout exhibited only minor adverse reactions. The primary behavioral changes were a decrease in swimming activity and a temporary loss of appetite. After 48 hours all fish resumed normal feeding and became progressively more active. No mortalities occurred in any of the replicated experiments, and all fish behaved normally when the experiments were terminated at 120 hours Murray and Ziebell (1984).

Table 20: Reactions of 10 rainbow trout to various pH levels during gradual acclimation experiments (0.2 to 0.4 of a pH unit/day)

Day	pH Range	Reactions and Condition of Trout
1	8.6-8.9	Normal
2	8.9-9.2	Activity decreased but feeding normal
3	9.2-9.7	Activity further decreased but feeding continued
4	9.7-9.9	Minor distress shown but feeding continued
5	9.9-10.3	Some fish lost equilibrium at 10.0, and feeding ceased. Loss of equilibrium increased at 10.1 and eyes of some fish developed corneal opacities; 50% of fish lost equilibrium at pH 10.2 and mortality was 60% at pH 10.3

Source: Murray and Ziebell (1984)

4.3 Effects of Low pH

“Chronic effects of low pH on fish populations may occur at pH levels that are not toxic to adult fish but that impair reproduction, and ultimately lead to population extinction (Jordahl and Benson 1987).” A study was conducted by Weiner et al. (1986) to determine the effects of low pH on the reproductive success of rainbow trout. It was determined that exposure of adult salmonids to pH values below 5.5 negatively effected reproduction. Adult rainbow trout were exposed to pH 4.5, 5.0, 5.5, and 6.5-7.1 during the final 6 weeks of reproductive maturation. Weiner et al. found that pH values of 5.5 and below impaired the creation of eggs in females and sperm in males.

Jordahl and Benson (1987) report that reproductive failure occurred in adult brook trout due to low pH in a freshwater stream with pH levels ranging from 5.0-5.8, while trout in a reference stream with pH ranging from 6.1-7.2 did not experience reproductive failure. Additionally, brook trout were absent from a highly acidic freshwater stream with pH ranging from 4.7-5.4 leading Jordahl and Benson to conclude that breeding females may avoid acidic tributaries.

In addition to effecting adult salmonids, highly acidic freshwater (low pH) can have a detrimental effect on eggs and juvenile salmonids. Weiner et al. (1986) determined that juvenile rainbow trout mortality was greatly increased at pH levels of 5.5 and below, and that no eggs survived when exposed to pH levels below 4.5. Hulsman and Powels (1983) found the mortality of rainbow trout yolk-sac larvae approached 100% within 5 days of exposure to pH 4.6 and 5.4, whereas exposure to pH 6.0 resulted in less than 3% mortality.

Jordahl and Benson (1987) conducted a study to determine the effect of low pH on juvenile brook trout survival and found that survival rates were highest in a freshwater stream with pH values ranging from 6.1-7.2 and lower in acidified streams with pH levels of 4.7-5.8. At pH values of 5.0 and lower, growth was retarded and the development of yolk-sac larvae was considerably prolonged. Additionally, larval activity was depressed, pigmentation was reduced, and incomplete hatching was observed in streams with low pH values of 4.7-5.8, but not in the stream with pH ranging from 6.1-7.2. Jordahl and Benson concluded that mean pH values of 5.0-5.4 can cause acid stress on developing juveniles, while pH levels from 6.1-7.2 are above ranges that negatively effect juvenile brook trout development and survival.

REFERENCES

Armour, C.L. 1991. Guidance for evaluating and recommending temperature regimes to protect fish. U.S. Fish and Wildlife Service Biological Report 90(22). 13 pp.

Bell, M.C.. 1986. Fisheries handbook of engineering requirements and biological criteria. Fish Passage Development and Evaluation Program. U.S. Army Corps of Engineers. 209pp.

Bjornn, T. and D. Reiser. 1991. Habitat requirements of salmonids in streams. In Meehan, W. ed., Influences of Forest and Rangeland Management on Salmonids Fishes and Their Habitat. American Fisheries Society Special Publication 19. pp. 83-138.

Brett, J.R. 1952. Temperature Tolerance in Young Pacific Salmon, Genus Oncorhynchus. Pacific Biological Station, and Department of Zoology, University of Toronto. J. Fish Res. Board Can. 9(6): 265-308 + appendices.

Brett, J. R., and J.M. Blackburn. 1981. Oxygen requirements for growth of young coho (*Oncorhynchus kisutch*) and sockeye (*O. nerka*) salmon at 15C. Can. J. Fish. Aquat. Sci. 38:399-404.

Brungs, W.A., and B.R. Jones. 1977. Temperature criteria for freshwater fish: Protocol and procedures. Environmental Research Laboratory, Duluth, MN. U.S. Environmental Protection Agency. EPA-600/3-77-061. 136pp.

California Department of Fish and Game (CDFG). 2001. California’s Living Marine Resources: A Status Report. Leet, W.S., C.M. Dewees, R. Klingbeil, and E.J. Larson [eds.]. The Resources Agency. Sacramento, CA. December 2001. 552pp. + appendices. Available at: <http://www.dfg.ca.gov/mrd/status/steelhead_rainbow_trout.pdf>. Website accessed on July 21, 2004.

California Department of Water Resources (CDWR). 1988. Water temperature effects on Chinook salmon (*Oncorhynchus tshawytscha*) with emphasis on the Sacramento River: a literature review. Northern District Office Report, Red Bluff, California. 42pp.

Cobel, D.W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. Transactions of the American Fisheries Society. 90:469-474.

Dahlberg, M.L., D.L. Shumway, and P. Doudoroff. 1968. Influence of dissolved oxygen and carbon dioxide on swimming performance of largemouth bass and coho salmon. Journal of the Fisheries Research Board of Canada. 25(1):49-70.

Davis, G.E., J. Foster, C.E. Warren, and P. Doudoroff. 1963. The influence of oxygen concentration on the swimming performance of juvenile pacific salmon at various temperatures. Transactions of the American Fisheries Society. 92:111-124.

Davis, J.C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on canadian species: a review. Journal of the Fisheries Research Board of Canada. 32:2295-2332.

Dickerson, H.W. and D.L. Dower. 1995. *Ichthyophthirius multifiliis* and *Cryptocaryon irritans* (Phylum Ciliophora). In Woo, P.T.K. ed., Fish Disease and Disorders. ISBN 085198 823 7; p.181-227.

Durborow, R.M., A.J. Mitchell, and M.D. Crosby. 1998. Ich (White Spot Disease). Southern Regional Aquaculture Center, Delta Research and Extension Center, Mississippi State University. Stoneville, Mississippi. 6pp.

Eddy, R.M. 1971. The influence of dissolved oxygen concentration and temperature on the survival and growth of Chinook salmon embryos and fry. Masters of Science Thesis. Oregon State University. Corvallis, Oregon. 45pp.

Elliott, J. 1981. Some aspects of thermal stress on freshwater teleosts. In Pickering, A.D. ed., Stress and Fish: Academic Press, London, p. 209-245.

Fischer, R.J. 1963. Influence of Oxygen Concentration and of its Diurnal Fluctuations on the Growth of Juvenile Coho Salmon. Masters of Science Thesis. Oregon State University. Corvallis, Oregon. 48pp.

Gale, W.L., A.G. Maule, A. Postera, and M. Peter-Swihart. 2001. Effects of Supersaturated Water on Reproductive Success of Adult Salmonids. Bonneville Power Administration project no. 2000-58. December 2, 2001. 33 pp.

Garside, E.T. 1966. Effects of oxygen in relation to temperature on the development of embryos of brook trout and rainbow trout. J. Fish. Res. Bd. Canada 23(8)1121-1134.

Hallock, R.J., R.F. Elwell, and D.H. Fry, Jr. 1970. Migrations of adult king salmon *Oncorhynchus tshawytsca* in the San Joaquin Delta as demonstrated by the use of sonic tags. California Department of Fish and Game, Fish Bulletin 151. 92pp.

Hassler, T.J. 1987. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Southwest). Coho Salmon. U.S. Fish and Wildlife Service Biological Report 82(11.70). U.S. Army Corps of Engineers, TR EL-82-4. 19pp.

Herrmann, R.B. 1958. Growth of juvenile coho salmon at various concentrations of dissolved oxygen. Masters of Science Thesis. Oregon State University. Corvallis, Oregon. 82pp.

Herrmann, R.B., C.E. Warren, and P. Doudoroff. 1962. Influence of oxygen concentration on the growth of juvenile coho salmon. Transactions of the American Fisheries Society. 91:155-167.

Holt, R.A., J.E. Sanders, J.L. Zinn, J.L. Fryer, and K.S. Pilcher. 1975. Relation of Water Temperature to *Flexibacter columnaris* Infection in Steelhead Trout (*Salmo gairdneri*), Coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) Salmon. J. Fish. Res. Board Can. 32:1553-1559.

Hulsman P.F. and P.M. Powles. 1983. Mortality of Walleye Eggs and Rainbow Trout Yolk-Sac Larvae in Low-pH Waters of the LaCloche Mountain Area, Onterio. Transactions of the American Fisheries Society. 112:680-688.

Jordahl and Benson, 1987. Effect of Low pH on Survival of Brook Trout Embroys and Yolk-Sac Larvae in West Virginia Streams. Transactions of the American Fisheries Society. 116:807-816.

Konecki, T.C., C.A. Woody, and T.P. Quinn. 1995a. Temperature preference in two populations of juvenile coho salmon, *Oncorhynchus kisutch*. Northwest Science. 69 (2): 417-421.

Konecki, T.C., C.A. Woody, and T.P. Quinn. 1995b. Critical thermal maxima of coho salmon (*Oncorhynchus kisutch*) fry under field and laboratory acclimation regimes. Can. J. Zool. 73:993-996.

Leitritz, E. and R.C. Lewis. 1976. Trout and salmon culture. California Department of Fish and Game. Fish Bulletin 164. 197pp.

Ligon, F., A. Rich, G. Rynearson, D. Thornburgh, and W. Trush. 1999. Report of the Scientific Review Panel on California Forest Practice Rules and Salmonid Habitat: Prepared for the Resource Agency of California and the National Marine Fisheries Sacramento, Calif. 92pp. + appendices.

Marine, K.R., and J.J. Cech. 2004. Effects of High Water Temperature on Growth, Smoltification, and Predator Avoidance in Juvenile Sacramento River Chinook Salmon. North American Journal of Fisheries Management 24:198-210.

McMahon, T.E. 1983. Habitat suitability index models: Coho salmon. U.S. Department of Interior, Fish and Wildlife Service. FWS/OBS-82/10.49. 29pp.

Mesa, M.G., L.K. Weiland, and A.G. Maule. 2000. Progression and Severity of Gas Bubble Trauma in Juvenile Salmonids. Transactions of the American Fisheries Society. 129:174-185.

Murray and Ziebell. 1984. Acclimation of Rainbow Trout to High pH to Prevent Stocking Mortality in Summer. The Progressive Fish-Culturist. 46(3):176-179.

Murray, C.B., and J.D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. Can. J. Zool. 66:266-273.

Myrick C.A., and J.J. Cech. 2001. Temperature Effects on Chinook Salmon and Steelhead: a Review Focusing on California's Central Valley Populations. Bay-Delta Modeling Forum. Technical Publication 01-1. 57pp.

Nielsen, J.L., T.E. Lisle, and V. Ozaki. 1994. Thermally stratified pools and their use by steelhead in Northern California streams. Transactions of the American Fisheries Society, 123:613-626. Available at: <http://www.humboldt.edu/~storage/pdfmill/Batch_9/thermally.pdf >. Website accessed on August 27, 2004.

Oregon Department of Environmental Quality (ODEQ). 1995a. Temperature: 1992-1994 Water quality standards review. Final Issue Paper. 122pp. Available at: <http://www.fishlib.org/Bibliographies/waterquality.html>. Website accessed on August 20, 2004.

Oregon Department of Environmental Quality (ODEQ). 1995b. Dissolved Oxygen: 1992-1994 Water quality standards review. Final Issue Paper. 166pp. Available at: <http://www.fishlib.org/Bibliographies/waterquality.html>. Website accessed August 20, 2004.

Pacha, R.E. and E. J. Ordal. 1970. Myxobacterial diseases of salmonids. In Snieszko, S.F. ed., A symposium on diseases of fishes and shellfishes. Special Publication No. 5, American Fisheries Society, Washington, D.C. p.243-257.

Piper, R.G., I.B. McElwain, L.E. Orme, J.P. McCraren, L.G. Fowler, and J.R. Leonard. 1982. Fish hatchery management. U.S. Department of Interior, Fish and Wildlife Service, Washington D.C. 517 pp.

Reutter, J.M. and C.E. Herdendorf. 1974. Laboratory Estimates of the Seasonal Final Temperature Preferenda of Some Lake Erie Fish. Presented at the 17th Conference for the International Association for Great Lakes Research. Center for Lake Erie Area Research, Ohio State University. Columbus, Ohio. Clear Technical Report No. 20. 13pp. + figures & tables.

Shumway, D.L., C.E. Warren, and P. Doudoroff. 1964. Influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. Transactions of the American Fisheries Society. 93:342-356.

Silver, S.J., C.E. Warren, P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and Chinook salmon embryos at different water velocities. Transactions of the American Fisheries Society. 92(4):327-343.

Spence, B.C., G.A. Lomicky, R.M. Hughes, and R.P. Novitzki. 1996. An ecosystem approach to salmonid conservation. TR-4501-96-6057. ManTech Environmental Research Services Corp., Corvallis, OR (Available from the National Marine Fisheries Service, Portland, OR). 356pp.

Spoor, W.A. 1990. Distribution of fingerling brook trout, ,*Salvelinus fontinalis* (Mitchill), in dissolved oxygen concentration gradients. J. Fish. Biol. 36:363-373.

Strange, J. 2006. Adult Chinook Salmon Migration in the Klamath River Basin: 2005 Sonic Telemetry Study Report (DRAFT). Yurok Tribal Fisheries Program, and School of Aquatic and Fishery Sciences- University of Washington in collaboration with Hoopa Valley Tribal fisheries. April 2006. 93pp.

Sullivan K., D.J. Martin, R.D. Cardwell, J.E. Toll, and S. Duke. 2000. An analysis of the effects of temperature on salmonids of the Pacific Northwest with implications for selecting temperature criteria. Sustainable Ecosystems Institute. Portland, OR. 147 pp. Available at: <http:/www.sei.org/pub.html# reports>. Website accessed on June 11, 2004.

Thomas, R.E., J.A. Gharrett, M.G. Carls, S.D. Rice, A. Moles, and S. Korn. 1986. Effects of Fluctuating Temperature on Mortality, Stress, and Energy Reserves of Juvenile Coho Salmon. Transactions of the American Fisheries Society 115:52-59.

Udey, L.R., J.L. Fryer, and K.S. Pilcher. 1975. Relation of water temperature to ceratomyxosis in rainbow trout (*Salmo gairdneri*) and coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 32:1545-1551.

U.S. Environmental Protection Agency (USEPA). 1986a. Ambient Water Quality Criteria for Dissolved Oxygen. Office of Water. EPA 440/5-86-003. 46pp.

U.S. Environmental Protection Agency (USEPA). 1986b. Quality Criteria for Water. Office of Water. EPA 440/5-86-001. 477pp. Available at: <http://epa.gov/waterscience/criteria/goldbook.pdf>. Website accessed August 12, 2005.

U.S. Environmental Protection Agency (USEPA). 1999a. A review and synthesis of effects of alternation to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. Region 10, Seattle, WA.

EPA 910-R-99-010. 279pp. Available at: <http://www.critfc.org/tech/EPA/report.htm>. Website accessed on June 11, 2004.

U.S. Environmental Protection Agency (USEPA). 1999b. 1999 Update of Ambient Water Quality Criteria for Ammonia. Office of Water. EPA-822-R-99-014. 147pp.

U.S. Environmental Protection Agency (USEPA). 2001. Issue Paper 5: Summary of technical literature examining the effects of temperature on salmonids. Region 10, Seattle, WA. EPA 910-D-01-005. 113pp. Available at: <http://yosemite.epa.gov/R10/water.nsf>. Website accessed on July 2, 2004.

U.S. Environmental Protection Agency (USEPA). 2003. EPA Region 10 Guidance for Pacific Northwest State and Tribal Water Quality Standards. Region 10, Seattle, WA. EPA 910-B-03-002. 49pp. Available at: <http://www.epa.gov/r10earth/temperature.htm>. Website accessed on June 23, 2004.

Washington State Department of Ecology (WDOE). 2002. Evaluating Criteria for the Protection of Freshwater Aquatic Life in Washington’s Surface Water Quality Standards: Dissolved Oxygen. Draft Discussion Paper and Literature Summary. Publication Number 00-10-071. 90pp.

Wagner, E.J., T. Bosakowski, and S. Intelmann. 1997. Combined Effects of Temperature and High pH on Mortality and the Stress Response of Rainbow Trout after Stocking. Transactions of the American Fisheries Society. 126:985-998.

Weiner G.S., C.B. Schreck, and H.W. Li 1986. Effects of Low pH on Reproduction of Rainbow Trout. Transactions of the American Fisheries Society. 115:75-82.

Welsh, H.W., Jr., G.R. Hodgson, B.R. Harvey, and M.F. Roche. 2001. Distribution of juvenile coho salmon in relation to water temperatures in tributaries of the Mattole River, California. North American Journal of Fisheries Management 21:464-470.

Whitmore, C.M., C.E. Warren, and P. Doudoroff. 1960. Avoidance reactions of salmonid and centrarchid fishes to low oxygen concentrations. Transactions of the American Fisheries Society. 89:17-26.

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

IMPORTANCE OF ESTUARINE REARING TO CENTRAL CALIFORNIA STEELHEAD (*ONCORHYNCHUS MYKISS*) GROWTH AND MARINE SURVIVAL

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF ARTS

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Morgan H. Bond

June 2006

The Thesis of Morgan H. Bond
is approved:

Professor Mark Carr, Co-Chair

Adjunct Professor R. Bruce MacFarlane,
Co-Chair

Professor Pete Raimondi

Lisa C. Sloan
Vice Provost and Dean of Graduate Studies

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

IMPORTANCE OF ESTUARINE HABITAT TO CENTRAL CALIFORNIA STEELHEAD (*ONCORHYNCHUS MYKISS*) GROWTH AND MARINE SURVIVAL

Morgan H. Bond

ABSTRACT

Estuaries are important rearing areas for many juvenile fishes and invertebrates. Often viewed as nursery habitats, estuaries are productive waters affording high growth potential and protection from predation. Juvenile anadromous salmonids move through estuarine waters during their annual migration from stream habitats to ocean waters where maturation occurs. In central California, near the southern extent of the steelhead (*Oncorhynchus mykiss*) range, estuaries often form seasonal freshwater lagoons, primarily during summer low flow conditions. To investigate the role that estuaries play in southern steelhead survival, I monitored juvenile size and growth and size at ocean entry of returning adults in Scott Creek, a representative central California coastal stream. During the annual spring emigration, the largest smolts (>150 mm fork length) move directly to sea, while some of the smaller smolts remain in the estuary until sandbar formation creates a closed freshwater lagoon. They remain in estuarine habitat at least until bar breakage during winter storms. High growth rates in the estuarine lagoon throughout the summer result in a doubling of fork length from the time of estuary entry (mean FL of spring migrants-112 mm, mean FL of fall lagoon resident-206 mm). Morphological analysis of returning adult steelhead scales indicates that there is strong size-dependent mortality at sea. Based

upon tagged recaptures and scale samples, estuary-reared steelhead show a large survival advantage and comprise 85% of the returning adult population despite being between 8% and 48% of the juvenile population. Although the Scott Creek estuary comprises less than 5% of the watershed area, it is critical nursery habitat, as estuary-reared juveniles make a disproportionate contribution to the spawning adult pool.

ACKNOWLEDGEMENTS

I would like to thank my committee Dr.'s Mark Carr, Pete Raimondi and R. Bruce MacFarlane for their helpful suggestions and guidance during the course of this study. I owe a great deal of gratitude to Mark Carr for his support and providing a diverse education throughout my graduate and undergraduate career. Bruce MacFarlane was also instrumental in facilitating my graduate research with advice, the freedom to pursue my interests, and the necessary funding to carry out this study.

In addition, I need to thank Sean Hayes, an honorary fourth advisor whose door was always open, and was subjected to many drafts of this thesis. Sean always found the time and funding that allowed me to finish this research. Fellow student Chad Hanson was also fundamental in facilitating this research and helping me form many of the ideas investigated in this thesis.

This project required an enormous amount of field and lab work over the course of the last four years. I owe a great deal to the huge crew of student employees, interns and volunteers who have committed their valuable time to this project. Special thanks is required for Chris Donohoe, Ellen Freund, Arnold Ammann, Jeff Harding, and Robert Baertsch who have committed more time helping me than they bargained for. The Monterey Bay Salmon and Trout Project, but especially Dave Streig and Al Smith, as well as Big Creek Lumber and Cal Poly San Luis Obispo were also gracious in allowing me access to their land and facilities, without which, this work could not have been done.

I also need to thank fellow lab mates in the Raimondi-Carr consortium, and members of the 2003 EEB grad student cohort for their help, support, and friendship. I would also like to thank my family for being a constant source of inspiration throughout my graduate career. Finally, I need to thank my partner and best-friend, Letitia Conway-Cranos, for sharing the highs and lows of ecological research and grad school, and being supportive through it all.

Funding for this research was provided by: The National Marine Fisheries Service, The Packard Ocean Science and Technology IMS Endowment, The Friends of Long Marine Laboratory, The Myers Marine Biology and Oceanographic Trust, and the PADI foundation.

INTRODUCTION:

Pacific salmon, including both semelparous salmon and iteroparous steelhead, are born in freshwater rivers and streams, and eventually move to the ocean to grow and mature before returning as adults. Because of their anadromous nature, salmonids inherently encounter several distinctly different habitats throughout their life-history. The effects of differential habitat use on growth and survival of individuals may play large roles in their recruitment to the adult population, and has been the focus of extensive study (Reimers 1973; Mitro and Zale 2002; Harvey et al. 2005).

During their seaward migration salmon may enter estuarine habitats, which vary widely in their physical characteristics (Healey 1991). Estuaries are of particular interest because they have been found to be nursery habitats for many species of fishes and invertebrates (Sogard 1992; Yamashita et al. 2000; Epifanio et al. 2003; Le Pape et al. 2003; Brown 2006). These nurseries provide a productive area that allows juveniles who use them to recruit disproportionately to the adult population compared to those from other habitats, because of the increased growth and survival nurseries afford (Beck et al. 2001). Salmon utilizing estuarine habitats have been well documented for rivers from British Columbia to central California (Reimers 1973; Levy and Northcote 1982; Dawley et al. 1986; McCabe et al. 1986; MacFarlane and Norton 2002). However, the time spent in an estuary, and the benefits received from that habitat may vary widely among species and watersheds. Some salmon move through estuaries in days, while others remain for months (Reimers 1973; Myers and

Horton 1982; MacFarlane and Norton 2002; Miller and Sadro 2003; Bottom et al. 2005).

Several theories have been proposed to explain why salmon may choose to remain in estuarine waters, postponing their eventual ocean migration. Estuaries can be extremely productive and may provide excellent opportunities for growth due to a complex invertebrate prey community and warmer water temperatures that cannot be found in freshwater tributaries (Boehlert and Yoklavich 1983; Macdonald et al. 1987; Shreffler et al. 1992). Estuaries may also provide a habitat where young salmon can avoid predation because visual predators may be limited by the potentially turbid nature of estuarine waters (Simenstad et al. 1982; Gregory 1993; Thorpe 1994)). Finally, because the physiological adaptation from a freshwater to a marine environment can be energetically costly, the estuary may provide a transition zone where fish can acclimate to increasing salinity before entering the ocean (Iwata and Komatsu 1984).

Estuaries of smaller coastal watersheds in the southern margin of North American Pacific salmon and steelhead distributions commonly form ephemeral freshwater lagoons. These lagoons are the products of low summer flow regimes that cannot displace ocean sand deposition at the estuary mouth. Eventual formation of a sandbar effectively blocks surface connectivity with the ocean, and reduces the tidal influence on the system, creating a warm, mostly freshwater, slow moving body of deep water. Summer temperatures in these systems can be substantially greater than temperatures in upstream tributaries, and may at times be near the thermal tolerance limit of steelhead (~25° C) (Myrick and Cech 2004). Lagoon conditions are generally present until the first winter freshet[1] increases stream flow and removes the sandbar, opening the estuary to the ocean. The development of lagoon conditions and their effects on salmonids is not well understood, although a recent study has shown a lagoon[2] environment to be beneficial to the growth of steelhead in central California (Hayes, unpublished data). Steelhead hatch in upstream waters and tributaries of creeks and spend some portion of time there before migrating toward the ocean. Many move quickly through estuary and enter the ocean, while others remain in the estuary habitat for an additional 6-9 months before ocean entry.

Throughout much of their range, steelhead populations continue to decline despite a federal Endangered Species Act (ESA) listing. This loss has been attributed to habitat loss, water loss and poor land management (Nehlsen et al. 1991; Busby et al. 1996). Still, the factors effecting steelhead population dynamics are not well understood, and few studies have looked at juvenile rearing habitats and their effect on survival for these threatened populations. Ward and Slaney (1989) found a strong size-dependent ocean survival in British Columbia's Keogh River steelhead, with the largest smolts exhibiting a higher survival than the smaller migrants. In their landmark study of central California coastal steelhead, Shapovalov and Taft (1954) suspected the Waddell Creek estuary as potential beneficial rearing habitat:

---

[1] A freshet refers to the sudden large increase in stream flow resulting from locally heavy rains.

[2] To avoid confusion, further reference to the physical space that forms either an open estuary in the winter and spring, or closed lagoon in the summer and fall is referred to as estuary habitat regardless of its condition.

"It is possible that the fish of the age 1 group have a strong tendency to stay in the lower stream and lagoon in order to make use of the extremely favorable living conditions there, while the fish of the age 2 group have reached a size where they can most favorably make use of the growing conditions found in the ocean."

However, neither Ward and Slaney (1989), nor Shapovalov and Taft (1954) were able to attribute survival of returning adults to a particular juvenile rearing habitat. Although young steelhead have been observed in estuaries (Dawley et al. 1985; Quinones and Mulligan 2005), the effects of that habitat on juvenile-to-adult survival has not been evaluated. Higher ocean survival of estuary-reared steelhead would implicate the estuary as an important nursery habitat despite its small proportion of all freshwater habitats. In light of population declines it is necessary to make the link between individuals that recruit to the reproductive population, and the factors that may have lead to their survival.

In this thesis, I address several questions to determine whether coastal California estuaries may serve as juvenile steelhead nursery habitats: *Do steelhead from Scott Creek exhibit evidence of size-selective survival at sea*? *Are emigrating steelhead from estuarine and upstream habitats different sizes upon ocean entry? Do juvenile steelhead experience differential growth between upstream and estuarine habitats?* and *Do estuarine reared steelhead have a disproportionately higher ocean survival than those from exclusively upstream habitats?* To investigate these questions, I have quantified the size distribution and abundance of downstream migrants and estuary-reared juvenile steelhead. I compared those data to the juvenile characteristics of surviving adults using scale morphologies to determine what contribution estuary-reared steelhead made to the adult population. In addition, I used passive integrated transponder (PIT) tags to monitor juvenile-to-adult survival rates of individuals from both estuarine and upstream habitats.

METHODS

Study System:

Scott Creek is a small coastal California watershed draining approximately 75km^2. It empties into the Pacific Ocean 80km south of San Francisco (37° 02' 28" N and 122° 13' 50" W) (Figure 1). Large waterfalls form impassable barriers on each of the main tributaries, thereby restricting access by anadromous fish to just 23 km of stream. Flow in Scott Creek is highly variable with peak winter flows reaching 28 m^3 s^{-1} (Hayes, unpublished data). Summer and autumn flows, however, may be reduced to 0.08 m^3 s^{-1} during an average year, and during extreme droughts the stream may run dry in the lower reaches. Substratum throughout the watershed is mudstone cobble with the exception of the Big Creek tributary, which is partially granitic cobble. The upper portion of the watershed is comprised of a high gradient stream dominated by a thick coastal redwood (*Sequoia sempervirens*) canopy. The lower gradient main stem of the creek has a lower density overstory cover primarily produced by alders (*Alnus sp.*), with understory dominated by willows (*Salix sp.*). An area of low-lying stream near the ocean forms a small estuary, which is subject to periods of high salinity during large tidal and swell events. The estuary is surrounded by a bullrush (*Scirpus californicus*) marsh. Like many coastal California streams, a sandbar forms each summer or fall, which causes the estuary to become a freshwater lagoon with infrequent saltwater input from ocean surges.

Native fishes of Scott Creek include steelhead, coho salmon (*Oncorhynchus kisutch*), threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), coastrange sculpin (*Cottus aleuticus*), and tidewater goby (*Eucyclogobius newberryi*). Juvenile starry flounder (*Platichthys stellatus*), and Pacific staghorn sculpin (*Leptocottus armatus*) are infrequently observed in the estuary. A small conservation hatchery has been operated continuously on Scott Creek since 1982, spawning a small number of steelhead and coho salmon each spring that are at least one generation removed from the hatchery (Hayes et al. 2004). Like many southern populations, steelhead in Scott Creek are listed as threatened by the ESA because of low population numbers, despite a relatively unaltered watershed.

Species:

Steelhead, *Oncorhynchus mykiss,* also known as the sea-run rainbow trout, is an anadromous fish endemic to much of the western coast of North America. Although it shares the *Oncorhynchus* genus with seven species of Pacific salmon, all salmon are semelparous, whereas steelhead have the potential to be iteroparous and will return to the ocean after spawning if possible. Like salmon, steelhead have the ability to move between fresh and saltwater through a series of physiological changes that alter the function of their osmoregulatory system. Adult steelhead in central California return from the ocean and begin entering the stream in the winter, following the first freshet (usually late December or early January), with the numbers of returning adults peaking in February or March, and continuing through late April (Shapovalov and Taft 1954; Hayes et al. 2004). Adults spawn in loose gravel in the main stem and tributaries, and superimposition of redds (nests) may occur as preferred spawning habitat is used multiple times. Egg development time depends on water temperature, but juveniles are generally observed emerging from the gravel four to six weeks after spawning (Shapovalov and Taft 1954) (Figure 2). Upon emergence, juveniles begin exogenous feeding and may remain in the stream from one to four years as parr before beginning the downstream migration (Shapovalov and Taft 1954). Downstream migration of juvenile steelhead begins in the late winter and early spring as a response to lengthening days triggers some parr to undergo physiological, morphological and behavioral changes in preparation for ocean life, thus becoming smolts (Zaugg and Wagner 1973; Hoar 1976; Handeland and Stefansson 2001). The seaward migration of smolts generally peaks in late April or May. During migration, smolts encounter estuarine water just prior to ocean entry, and some percentage of the migrants remain in that habitat. Fish remaining in the estuary may continue to occupy that habitat for an additional 6-9 months before entering the ocean. Steelhead generally remain at sea for 1-2 years before returning to spawn, although a small percentage of spawners have spent three years in the ocean. It is generally unknown what ocean habitats are utilized by central California steelhead, but through limited ocean captures it is safe to assume that at least some adults move far offshore during their ocean migration (Burgner et al. 1992).

Methods Overview

To effectively demonstrate what influence the estuary has on the survival rate of steelhead at sea, it is important to sample both the juvenile and adult populations. Initially, I measured the strength of size-dependent ocean survival with a population of marked hatchery-reared smolts. Then, I monitored growth rates of wild fish in both upstream and estuary waters to examine the potential benefits of each habitat type. Additionally, I evaluated the abundance and size distribution of downstream migrating juveniles (smolts), and those fish that remained in the estuary area throughout the summer and fall. Some of the wild individuals were tagged for later identification to measure individual growth and survival rates. Finally, scale samples were taken from returning adults to identify the size at initial ocean entry and classify the juvenile rearing habitat (i.e., upstream or estuary) through scale morphology.

Estimation of the strength of size selective mortality at sea

In order to determine whether processes of size-selective ocean survival could be driving differential return rates of estuarine and upstream reared fish, I utilized a population of hatchery smolts released in the spring of 2003. I measured the fork length (FL) of 562 hatchery-raised smolts from a pool of 6880 individuals, one week prior to release from the hatchery. Hatchery fish in Scott Creek enter the ocean soon after release (Hayes et al. 2004), therefore I assume that the size distribution of hatchery fish prior to release closely resembled the distribution that entered the ocean. All fish released from the hatchery were adipose fin clipped to permanently mark their origin as hatchery-reared. Hatchery fish from the 2003 cohort that returned from the ocean as adults in the winter and spring of 2004 and 2005 as 1-and 2-year ocean fish were sampled to determine the size at ocean entry of surviving adults, and the extent of size-dependent survival. Initial size at ocean entry was back-calculated from scale samples using a method described below. The size at release of hatchery smolts was compared to the size at ocean entry of returning hatchery adults with a two-sample T-test to determine whether processes of size-dependent ocean survival were having a strong effect on the resulting adult population.

Sampling of Returning Adult Steelhead

To determine the strength of size-dependent mortality, adults that returned from the ocean in the winter and spring of 2004 and 2005 to spawn were sampled with a floating resistance panel weir, operated daily during the spawning run (Tobin 1994). The weir had a trap box with a one-way door to capture all steelhead moving upstream. The weir operated in stream flows up to 7 m^3 sec^{-1}, beyond which the resistance panels fold flat and allow water and debris to flow over the top. Although the successful operation of the weir was flow dependent, 60-80% of the returning adult population were successfully sampled during normal years, as determined by a mark-and-recapture estimate (Hayes, unpublished data). Upon capture each fish was identified as either hatchery or wild origin, measured to the nearest 0.5 cm FL, and weighed to the nearest 0.1 kg. A sample of 10-15 scales was taken from a standard area, just above the lateral line on a diagonal between the posterior attachment of the dorsal fin and the anal fin (Maher and Larkin 1954). All scale samples were positioned onto waxed weighing paper, which was placed in a labeled envelope and dried for preservation.

Scale Analysis

I used the relationship between fish size and scale size to determine the size at ocean entry of surviving hatchery adult steelhead from the 2003 smolt class. To prepare scale samples for analysis, each wax paper containing dried scales was removed from its envelope and placed under a dissection microscope. All scales were scanned to find the most original, uniform scale available. Original scales (compared to regenerated scales) have complete circuli forming concentric rings from the edge to the core, or focus, of the scale. Scales are also judged for uniformity of shape. Scales that are symmetrical and not overly oblique are preferred for analysis. Up to six of the most original and uniform scales were placed on slides, and flattened with a cover slip. Cover slips were fixed into place with transparent tape. Scales that were original and uniform, but too dirty to be accurately read, were placed into 1ml microcentrifuge tubes with de-ionized water. The tubes were then floated in an ultrasonic bath for 5 minutes at 37º C. Upon removal from the tubes, clean scales were dried on Kim-Wipes®, and quickly flattened on the slide with a cover slip and allowed to dry flat. Scales were photographed using a microscope mounted Nikon® digital camera (DXM1200 3840 x 3072 pixels). The most original, uniform scale from each slide was photographed and saved as an uncompressed TIFF file.

Once each scale had been photographed, OPTIMAS® software (Media Cybernetics, Inc., Silver Spring, MD) and a custom macro were used to analyze for: total scale radius (SR, the distance from the focus to the edge of the scale), radius at ocean entry (OER, the distance from the focus to the ocean entry check), number and spacing of each freshwater and ocean circulus, and number of ocean annuli (Figure 3). For ease of reading, all measurements were made 20º off of the longest axis. A qualitative score for each analysis was noted on a scale of 1-3, with a score of 1 being a very original, normally shaped scale with a high reading confidence. Only scales with a score of 1 or 2 were used in further analyses.

There is a strong relationship between fish size and scale size, therefore fish size can be back-calculated from scale size (Ricker 1992). The FL at initial ocean entry was back-calculated on scales from adult steelhead using a regression of FL on SR. The regression was created with original scales from 1251 juvenile and adult steelhead representing the complete range of sizes available. The relationship between SR and FL (Figure 4) is described by:

$$\text{(Eqn. 1)} \qquad \text{FL (mm)} = 0.1686\ \text{SR (microns)} + 34.872$$

$(R^2=0.97)$

An intercept of 34 mm agrees with other published values of FL at initial scale formation for *O. mykiss* (Snyder 1938; Kesner and Barnhart 1972; Hoplain 1998). There is some discussion in the literature as to the most appropriate method for back-calculation of size (Francis 1990; Panfili and Troadec 2002). However, the Fraser-Lee method is widely used, and recent studies have empirically demonstrated its reliability in several fish species, including *O. mykiss* (Davies and Sloane 1986; Klumb et al. 1999). I employed the Fraser-Lee method (Fraser 1916; Lee 1920) in all back-calculations using the formula:

$$L_{oe}=((L_c-c)(R_{oe}/R_c)+c) \quad \text{(Eqn. 2)}$$

where

L_{oe} = fork length at ocean entry of juvenile in mm

R_{oe} = Scale radius at ocean entry of juvenile in microns

L_c = fork length of adult at capture in mm

R_c = Scale radius of adult at capture in microns

c = intercept from (FL) on scale radius (SR) regression (Eqn. 1)

Size at ocean entry of upstream and estuarine reared juveniles

To determine whether juvenile steelhead from both upstream habitats and the estuary entered the ocean at different sizes and numbers, I trapped spring downstream migrants (smolts) each winter and spring (Jan.-June) and sampled the estuary population each fall (Oct.-Dec.). To determine both the number and size of downstream migrants, I placed a fyke net across the stream approximately 50m upstream of the estuary (Figure 1). The fyke net consists of a series of 91cm diameter steel hoops, covered in 6.4 mm (¼”) nylon mesh that are separated by mesh cones that allowed fish to enter but prohibit their escape. The net has two 1.2m tall seine type wings, which were affixed in the stream to produce a "V" shape and help collect downstream-moving fish in the net. The net was generally run three days per week; however, storm events periodically prohibited the net from being operated. To estimate the number of downstream migrants (N_m), I first calculated net efficiency (E) by releasing a known number of hatchery fish, which are assumed to move rapidly toward the ocean (Hayes et al. 2004) upstream of the net, and count the number captured (Table 2). Net efficiency was estimated as the percentage of hatchery fish caught, and used to estimate the number of wild downstream migrants with the following equation:

(Eqn 3) $$N_m=(C_m*365)/E$$

Where

N_m = Estimated number of downstream migrants

C_m = Mean daily catch

E= Trap efficiency (Number of hatchery fish caught/number of hatchery released)

Steelhead captured in the fyke net were placed in aerated buckets until sampling was complete. Each fish was measured to the nearest mm FL, and mass was measured to the nearest 0.01 gram. A sample of 10-15 scales was taken by running the blade of a pair of scissors in the posterior to anterior direction lightly along the side of the fish. Scales were routinely taken from the left side of each fish, but if there was damage to that area scales would be taken from the opposing side. All scales were placed on waxed weighing paper and dried for later analysis. Finally, each fish ≥65 mm FL was scanned for a Passive Integrated Transponder (PIT) tag, using a handheld tag reader (Allflex USA, Dallas Fort Worth Airport, TX.). If no tag was found, then one would be injected using a sterile 12 gauge needle. PIT tags carry a unique identification code so that each fish can be identified later for measurements of individual growth and survival. After sampling, fish were returned to an aerated black bucket to recover for a minimum of 10 minutes before release into the stream. All data was recorded on a Palm® handheld computer in the field, and was uploaded to a Microsoft Access® database daily.

The estuary habitat was sampled each summer and fall to determine both the population size and the size distribution of estuary juveniles just prior to ocean entry. The estuary habitat, which I define as the area from the beach at the mouth of Scott Creek to approximately 800 m upstream (Figure 1), was sampled monthly using a modified 30 m x 2 m nylon beach seine. A large 2 m x 2 m, 6.4 mm (¼”) mesh bag was sewn into the center of the seine to help collect fish in the deeper portions of the estuary where pulling the net onto land was not possible. The entire estuary was seined as thoroughly as possible in 50 m sections each month, with the exception of the upper 200 m. Extremely dense plant cover dominated the upper estuary and seining was impossible. All fish were placed into mesh containers in the estuary until all seining was complete, so that fish could not be collected twice. Estuary steelhead were sampled using the same protocol as trap captured downstream migrants.

However, the estimation of size at ocean entry required adjusting the size distribution of the last sampling each fall to account for growth occurring between the last sampling and sandbar breakage. To do this, growth rates from the last sampling event (see: Differential growth of estuary and upstream fish, below), and the number of days between the last sampling and bar breakage were calculated and added to the final fall size distribution. Because the size distributions of spring downstream migrants and estuary fish could not be compared statistically between years due to the change in sampling technique and varying trap effectiveness, all fish were grouped into only two distributions; spring downstream migrants, and fall estuary fish. These two distributions were compared with a two-sample T-test.

To estimate the population size in the estuary each fall, PIT tags were employed in a simple mark and recapture using the Petersen method (Roff 1973). After sandbar closure, I tagged a subset of the fish caught in the newly formed lagoon. In the month following the initial tagging, a new seining effort was performed to assess the number of tagged individuals present and estimate the population size. This process was repeated every month until winter rains made seining of the estuary impossible. The following equations were employed to estimate the estuary population size and variance:

(Eqn 4) $$N_e = C_e M_e / R_e$$

(Eqn 5) $$V(N_e) = (M_e^2 C_e (C_e - R_e)) / R_e^3$$

Where

N_e= Estimated estuary population size

M_e= Number of individuals marked in the first seining

C_e= Number of individuals captured in the 2nd seining

R_e= Number of individuals from the 2nd seining that are marked

$V(N_e)$= Variance of population estimate

Because there are few predators of steelhead in the estuary, mortality is assumed to be negligible in the time between the first and second seining efforts. A mark and recapture was not conducted prior to sandbar closure because of the possibility of individuals entering the ocean and leaving the population during that time. In addition, the number of downstream migrants entering the estuary drops rapidly after June, and I assumed new input to be negligible (Hayes et al. 2004).

In addition to determining the number of fish from the upstream and estuary habitats, it is important to determine how both size class, and date of estuary entry affect the resulting estuary population. To do this, I compared the size distribution of all downstream migrants with the size distribution at downstream migration of those PIT tagged individuals that stayed in the estuary after sand bar closure. Data were organized into 15 mm FL bins from 85 mm to 145 mm, with all fish greater than 145 mm being grouped into the last bin of >145 mm, and a Chi-squared test was used to compare the two distributions.

Sandbar closure often occurs in midsummer, late July or early August during years with normal rainfall. However, downstream migration of juvenile steelhead is usually complete by early July. The individuals that remain in the estuary throughout the summer are therefore not simply fish that began their migration too late, and were forced to remain in the estuary until sandbar breakage in the winter. To determine what effect timing of downstream migration had in determining what individuals remained in the estuary after sand bar closure, I compared the number of fish per day captured at the downstream migrant trap to the initial capture date for those PIT tagged individuals that remained in the estuary. The two resulting frequency-date distributions were compared with a two-sample T-test.

Differential growth between estuary and upstream habitats

To determine whether differential growth rates between the estuary and upstream habitats may be driving differences in size at emigration for the two populations I sampled fish in each habitat monthly. Upper watershed samples were collected at six sites in the upper watershed that were characteristic of the area and where juvenile steelhead were abundant (Figure 1). All sites were pool habitats that could be sampled effectively during low summer and fall stream flows, and are collectively referred to as upstream habitat, with no distinction between any of the sites. Fish were collected using a 3.2 mm (⅛”) mesh, 4 m x 1 m seine net, or hook and line. For both methods, all collected fish were placed in aerated buckets with fresh stream water until processing, and were sampled with identical methods to downstream migrants and estuary residents.

During regular monthly juvenile sampling at each of the six upstream sites and the estuary, all fish were scanned for PIT tags as an indication of previous handling. Fish with PIT tags were measured, and specific individual growth rates were calculated using the following equation:

$$\text{SPGR}=100 \times [\ln(L_2/ L_1)]/(D_2-D_1) \quad \text{(Eqn. 6)}$$

where

L_1 = FL at initial capture in mm

L_2 = FL at next successive capture in mm

D_1 = date of initial capture

D_2 = date of next successive capture

SPGR = specific growth rate (% change in FL/day)

A mean date of growth was assigned to each growth rate calculation as the midpoint between two fish measurement dates. Growth rates from fish at all upstream sampling locations were pooled, and mean growth rates for upstream fish and estuary fish were generated for each year. Growth rates for both 2003 and 2004 were grouped for each habitat, and were compared with a two sample T-test to look for differences in growth by habitat.

Finally, I investigated the relationship between mean fish growth and mean population density in the estuary after sandbar closure in 2003-2005 to explain potential differences between growth each year. To do this, I generated a regression of mean annual specific growth rate on mean annual estuary population size for each year from 2003-2005. Because the lagoon created by sandbar closure in the estuary each year is of similar size, I assume population size to be a good proxy for density.

Do estuary reared fish recruit disproportionately to the adult population compared to upstream reared individuals?

Size at ocean entry of returning adults

I used four methods to determine whether estuary fish were returning disproportionately to the returning adult population. In the first, I calculated the size at ocean entry of returning adults and compared that distribution with the sizes at ocean entry of emigrating juveniles. The second method involved the classification of returning adults to either upstream or estuary juvenile rearing habitat using a discriminant function analysis and measures of scale morphology. Additionally, I calculated return rates of adult steelhead that were PIT tagged as juveniles at one of the two habitats to determine relative survival rates for each habitat type. Finally, I analyzed scale microchemistry to determine whether elemental scale composition varied between scale growth in each of the two habitats, and whether that variation could be utilized to classify returning adults to freshwater habitat of origin.

I back-calculated the size at ocean entry of wild returning adult steelhead utilizing the same scale measurement technique that was employed in the calculation of size at ocean entry for returning hatchery fish. Scale samples were collected from 439 wild adults from spring of 2002 through spring of 2005. Although some 1-year ocean fish were captured and assigned to the 2004 ocean entry group, these samples were omitted from this analysis because of the potential bias of using only “early” returning fish to classify the entire 2004 cohort. After removals, 364 original, uniform, scale samples that received a score of 2 or better during reading were used for the final analysis. Because of the difficulties of identifying freshwater annuli in adult scales, especially in estuary residents, returning adult steelhead were not assigned to a particular downstream migrant cohort for comparison. Instead, all returning adults were grouped together as one class, and compared to grouped estuary fish and downstream migrants from all years. Analysis of variance (ANOVA) was conducted to evaluate the relationship between fish FL and fish type. The independent variable, fish type, had three categories: spring downstream migrant, fall estuary, and FL at ocean entry of returning adults. Fork lengths for each group were data for all sampling years combined. Fork length was the dependent variable.

Scale morphology DFA

In addition to size, I used circuli spacing and spacing variance to distinguish between adults reared as juveniles in the estuary and those reared upstream. Circuli spacing in scales is correlated with growth in both coho (*Oncorhynchus kisutch*) (Fisher and Pearcy 1990; Fisher and Pearcy 2005), and sockeye salmon (*Oncorhynchus nerka*) (Fukuwaka and Kaeriyama 1997), therefore it is reasonable to assume that the relationship holds true for steelhead as well. The origin of fish in mixed stocks of hatchery and wild steelhead has been determined successfully by differences in scale morphology attributable to different growth regimes in the hatchery and the wild (Maher and Larkin 1954; Bernard and Myers 1996; Tattam et al. 2003). To provide an indication of estuary-derived growth, I calculated the mean circuli spacing and variance for the last 18 circuli of juvenile fish of all size classes from the upper watershed and estuary. Although many combinations of circuli were tested in a stepwise fashion, the mean of the last 18 circuli was most effective at discriminating between prior habitat use, while simultaneously removing problems of non-independence in sampling. Upstream samples were collected throughout the year, but because individuals only use estuary habitat after a prior stay in the upper watershed, estuary samples were taken in the late fall when the estuary growth signature has been maximized. To separate upstream and estuary-reared juveniles, mean circuli spacing and the variance of circuli spacing were used in a discriminant function analysis (DFA). The mean spacing and variance of the last 18 freshwater circuli of scales from returning adults were then included in the DFA to classify the freshwater life-history path returning adults had utilized as juveniles.

Ocean survival of PIT tagged juveniles

In order to calculate the ocean survival of juvenile steelhead, I placed PIT tags in 640 steelhead at both the downstream migrant trap and the estuary in the spring and summer of 2003. Through mark and recapture, I was able to estimate the number of tagged fish that remained in the estuary after sandbar closure. Some returning adults in the winter and spring 2005 were carrying PIT tags from the 2003 deployment (Adults returning in 2004 were checked, but no tags were found.). I used estimates of the number of juvenile PIT tagged fish from each habitat, and the number of returning adults from each habitat to calculate the survival rate of fish from each habitat. In addition, scale morphology was analyzed for each returning adult to determine whether the number of ocean years expressed on each scale matched with expected time of ocean entry based on measured juvenile habitat use from PIT tag recaptures.

Scale microchemistry

In addition to patterns of morphology, I explored scale microchemistry to identify periods of estuary residence. Because fish live in an aqueous environment, they obtain the raw materials for growth from both their diet, and the surrounding water. As calcified tissues are formed, fish incorporate many elements present in the water in the proportion they are found in the environment. It is fortuitous that the abundance of these elements varies in different water masses. Scales, comprised of a calcium phosphate matrix, have successfully been used as a historical record of habitat use where water chemistry varies between discreet regions (Wells et al. 2003).

To test whether estuarine residence was recorded in scales as an area of mixing between fresh and oceanic water, I used scales collected from juvenile steelhead that were sampled just prior to their entrance into the estuary and compared these to scales collected from the same individuals after at least one month of estuarine residence. Scales were cleaned under a laminar flow hood by placing them in a microcentrifuge tube with 2mL of Millipore® Milli-Q ultrapure water. The microcentrifuge tubes were placed in an ultrasonic bath for 10 minutes to remove any surface material. Scales were removed from the microcentrifuge tubes and placed in a second, empty tube to dry. Dried scales were then mounted on petrographic slides with double sided tape (3M® 665 permanent-linerless double coated tape). Scale chemistry was analyzed with a VG Excel quadrupole inductively-coupled plasma mass spectrometer (ICP-MS) coupled with a 193 nm Excimer laser. Scales were pre-ablated with the laser to remove any possible surface contamination by running a laser transect from the focus to the edge along the same 20° offset that was used to measure scale morphology (travel rate: 60µm sec^{-1}, spot size: 70µm, firing rate:1Hz). The scale sample was collected for introduction to the ICP-MS immediately following pre-ablation by running a second transect along the original transect (travel rate: 5µm sec^{-1}, spot size:10µm, firing rate: 10Hz). Thirteen elements were targeted for analysis with the ICP-MS: ^{7}Li, ^{24}Mg, ^{43}Ca, ^{55}Mn, ^{65}Cu, ^{66}Zn, ^{88}Sr, ^{137}Ba, ^{138}Ba, ^{139}La, ^{140}Ce, ^{208}Pb, ^{238}U. Data were binned to generate a mean value for each five micron interval, and each element was converted to an elemental ratio with respect to calcium to account for differences in the amount of material introduced into the ICP-MS. Transects from multiple scales taken from the same individuals over time were compared to ascertain how stable the chemical signal of each habitat was, and whether those signals were strong enough to identify juvenile habitat use in returning adult steelhead.

RESULTS

Estimation of the strength of size selective mortality at sea

Hatchery smolts released in April of 2003 encountered strong size selective mortality at sea. Smolts measured just prior to release had a mean FL of 158 mm (SD=35). Few hatchery fish were observed in the stream two weeks after the release date, and hatchery fish were not found to use the estuary habitat (Hayes et al. 2004)

Original scales were obtained from hatchery fish returning as adults in the winter/spring of 2004 and 2005 as 1-and 2-ocean year fish, respectively. Back-calculation of FL at ocean entry indicated that the surviving adult population had a mean FL at ocean entry of 181.2 mm (SD=28.9), which was significantly larger upon ocean entry than the initial population of fish released from the hatchery (t(592)=4.47 p<0.001, Figure 5).

Size at ocean entry of upstream and estuarine reared juveniles

The mean FL of downstream migrating smolts in 2002 and 2003 was 110 mm. The mean FL of 2004 downstream migrants was 92 mm, however, net mesh size was changed from 9.5 mm (⅜”) to 6.4 mm (¼”) and the net became more effective at catching the smaller individuals that were not sampled in 2002 and 2003. Additionally, high flows in the spring of 2005 prevented net operation until late in the season, and early migrants were not sampled. Because of these discrepancies in sampling, I did not compare downstream migrant size distributions between years. The total number of downstream migrating steelhead is estimated for 2003 and 2004 (Table 1). No population size is estimated for 2002 or 2005 because of the lack of early season samples due to excessive stream flow.

The size distribution of the estuary population upon bar breakage each winter varied by year, mean FL upon winter sandbar breakage was largest in 2003 at 213 mm (SD=32), and smallest in 2004 at 182 mm (SD=26), but estuary fish from all years (2002-2005) were significantly larger than spring downstream migrating juveniles in the same years (t(455.4)=45.76 p<0.001, Table 2). The estuary population varied by year, but was between 8 (2004) and 48 (2003) percent of the downstream migrant population where estuary mortality is assumed to be low (Table 1).

Stay in estuary or go to sea?

Of the 298 fish I measured and PIT tagged at the downstream migrant trap in spring of 2003, 61 fish were recaptured in the estuary after sandbar formation in the fall. The initial FL at estuary entry was compared between the two groups of fish to determine what sizes of fish remained in the estuary. A Chi-Square test was used to compare the two distributions and a significant difference was found, indicating that the initial size of downstream migrants was larger than the initial size of those individuals that remained in the estuary $\chi^2(5, N=359)=15.36$ $p=0.009$. No fish with an initial estuary entry FL larger than 150 mm was observed after sandbar closure, indicating that those fish move to the ocean before bar formation (Figure 6). The mean downstream trap tagging date for all tagged fish and those that stayed in the estuary was not significantly different ($t(227)=0.490$, $p=0.625$) indicating that the timing of downstream migration did not have an effect on the resulting downstream migrant population, and fish from throughout the entire run inhabited the estuary after sandbar closure.

Differential Growth Between Estuary and Upstream Habitats

Specific growth in the estuary was significantly greater than upstream habitats for 2003 and 2004 ($t(501)=22.7$, $p<0.001$, Figure 7). Mean growth in the estuary for 2003 and 2004 was 0.36% increase in FL per day, while mean upstream growth was

0.06% increase in FL per day for the same period. A strong negative relationship between growth rate and population size among the three years sampled (R^2=0.99), suggests that estuary growth rate among years is at least partially explained by differences in steelhead density among years (Figure 8).

Do estuary reared fish recruit disproportionately to the adult population compared to upstream reared individuals?

Size at ocean entry

To determine whether returning adults were recruiting disproportionately from one of the two general habitats, I compared the size at ocean entry of the two juvenile groups from 2002-2005 with the size at ocean entry of returning adults from the same years (Figure 9). For all sampling years combined, FL at ocean entry differed significantly among the spring downstream migrants, fall estuary residents, and back-calculated returning adults (ANOVA: F(2, 1802)=2192.9, $p<0.001$). Post-hoc comparisons using the Tukey test indicated that there were significant differences among all three groups. However, the mean FL of spring downstream moving smolts for all years was 106 mm (SD=26, n=1108), while fall estuary fish was 198 mm (SD=33, n=331), and ocean entry FL of returning adults was 208 mm (SD=38, n=364).

Habitat Classification by Circuli Spacing

In order to provide another independent measure of juvenile freshwater rearing habitat of returning adult steelhead, I used measures of scale spacing as a proxy for juvenile growth, with large spacing indicating faster growth and estuary residence, and smaller spacing indicating lower growth and upstream residence. Mean circuli spacing of the last 18 circuli of scales from estuary (n=96) and upstream juveniles (n=92) were log transformed. Spacing was significantly different between upstream and estuary fish (t(186)=13.95 p<0.001, Figure 10). A discriminant function analysis (DFA) using mean spacing and variance of spacing of the last 18 freshwater circuli as predictors was performed to assign juveniles to their respective rearing habitat. The DFA jackknifed classification indicated an 86% correct assignment (83% for estuary, 90% for upstream) to either habitat. Scales from all adult fish with a reading score of two or better (n=406) were analyzed to determine the mean spacing and variance for the last 18 circuli prior to ocean entry. Spacing was significantly wider than either the estuary or upstream individuals F(2, 593)=151.8, p<0.001, Tukey post-hoc test. The DFA was then used to assign returning adult steelhead to one of the two juvenile rearing habitats (Upstream or Estuary) based upon the same parameters used to in the juvenile habitat assignment (mean spacing of the last 18 circuli, variance of spacing). Of the 406 adults analyzed, the DFA jackknifed classification matrix assigned 61 ±9 (15%) returning adults to upstream juvenile habitat, while 344 ±48 (85%) were assigned to estuary juvenile rearing habitat.

Pit Tag Recaptures and Survival

I estimated through mark and recapture that 1 in 10 steelhead in the estuary was carrying a PIT tag by December of 2003. In winter and spring of 2005, 142 returning adult steelhead were sampled. Thirteen adults (7 males, 6 females) were carrying PIT tags implanted when they were juveniles. All 13 individuals were observed in the estuary in 2003. Scale analysis indicated that all of the tag-carrying adults had only one year of growth in the ocean, indicating that they had not entered the ocean until spring of 2004. In addition, the PIT tagged adults maintained nearly the same tag ratio (1:10.9) in the returning adult population that I observed in the estuary in 2003, indicating that it is probable that many of the returning adults not carrying tags were also products of the estuary juvenile rearing environment.

Ocean survival of all Scott Creek steelhead from 2003 was estimated from the percentage of PIT tag recaptures from adults captured in winter of 2005 and 2006 (no 2003 tagged steelhead were captured in 2004). Thirteen tags were recovered in 2005, however, only 78% of returning steelhead were sampled (Hayes, unpublished data), which indicates that approximately 17 tagged steelhead returned that year. In addition, 4 tags were recovered in 2006, however, since the 2006 adult return season has not yet ended, there is no sampling efficiency currently available for 2006. A total of 640 juveniles were tagged at both the downstream migrant trap and the estuary in 2003, which indicates a population-wide smolt-to-adult survival rate of at least 3.3%. However, all tags recovered were from estuary-reared fish, as revealed by tagging histories and scale analysis. I estimate that there were 254 tagged fish utilizing the estuary habitat in the fall of 2003 from the population size (2540) and the ratio of tagged to untagged fish (1:10). This indicates an 8.3% survival of the estuary-reared population.

Scale Microchemistry

Ratios of each elements or isotope to calcium along scale focus-to-margin transects were plotted for each fish to compare before and after estuarine growth samples. Most elements showed no significant change in ratio upon estuary entrance. However, the Mn:Ca and ^{138}Ba:Ca ratios showed changes in their elemental ratios after estuary entrance (Figure 11). Unfortunately, these data also indicate that there is only partial stability between the samples, and previous signatures had been altered in the time between when each sample was taken. Given the short time between the first and second scale samples from each individual and the relative instability of chemical content, I can conclude that the chemical composition is likely not stable enough to retain signatures of estuary residence throughout the entire ocean phase.

DISCUSSION

This study provides evidence for the importance of estuarine habitat to central California steelhead populations. A strong size-dependent ocean survival coupled with a large dichotomy in sizes between estuary and upstream-reared smolts, has led to a large survival advantage for the larger estuary-reared individuals. These patterns are driven by the difference in growth rates between productive estuary waters and the relatively oligotrophic upstream habitat.

Estimation of the strength of size selective mortality at sea

Although evidence of size selective survival is not new (Sogard 1997), the strength of size selective survival coupled with an extreme dichotomy in sizes of ocean entry between the two general rearing habitats (upstream tributaries and estuary) could lead to size selective survival being the largest determinant in driving which individuals ultimately return to the adult population. Back-calculated size at ocean entry for 2003 hatchery juveniles as adults returning in 2004 and 2005 indicated that small hatchery smolts (≤150 mm FL) were underrepresented in the returning adult population, and larger smolts (>200 mm) were overrepresented. These data support the size-biased survival proposed by Ward and Slaney (1989) for a northern stock of steelhead. Because few hatchery fish were observed in the upper watershed or estuary after planting, I assume that fish of all sizes completed the ocean migration and the resulting ocean-entry size distribution of returning adults was created through size-dependent selection in the marine environment. It has been shown that hatchery-reared salmon may experience lower overall survival in the marine environment (Jonsson et al. 2003). Although this inherent difference in smolt quality could be driving the size-biased survival in the resulting returns, I would argue that although hatchery fish may suffer a lower overall survival, the processes shaping the size distribution of surviving fish (i.e., predation, foraging success) should act similarly on both hatchery and wild populations. This would suggest that wild Scott Creek smolts should also experience a strong size-biased survival.

Size at ocean entry of upstream and estuary reared juveniles

Downstream migration

Spring downstream migrants enter the Scott Creek estuary at a relatively small size compared to smolting steelhead in more northern populations (Ward and Slaney

1988) (Figure 9). This is consistent with the relatively low growth rates observed in upstream habitats of Scott Creek (Hayes et al. 2006, unpubl. data), and what was observed by Shapovalov and Taft (1954) in nearby Waddell Creek. While the estimated number and mean size of downstream migrants differed annually (due to both a change in net mesh size and differences in flow affecting the number of days the net could be operated each year), these differences are minimal and still indicate that the vast majority of Scott Creek steelhead move downstream at a very small size.

Estuary Residence

The estuary population of steelhead is comprised of juveniles that emigrated from the upper watershed in the spring and summer. The largest downstream migrants (>150 mm FL) move through the estuary and are not observed again as juveniles, indicating that they are large enough to move directly to sea without additional growth. It is certainly possible that young steelhead in Scott Creek are migrating at a small size specifically to take advantage of the favorable estuary growth potential. The estuary population each fall varied between 8 and 48% of the estimated total number of downstream migrants (in 2004 and 2003, respectively). However, 48% estuary utilization in 2003 is probably an overestimate, because a large mesh size was used in the downstream migrant trap that year, effectively underestimating the number of downstream migrants. Timing of sandbar formation does appear to impact the overall number of downstream migrants that will reside there. In years when high flow prevents early season sandbar formation, productive deep water is not found until the late summer and may harbor fewer fish. On the other hand, early sandbar formation during low flow years leads to productive habitat being available during peak downstream migration, and may cause more fish to remain in the estuary throughout the summer.

Differential growth between estuary and upstream habitats

Growth rates in the estuary are extremely high, nearly 10 times what is observed in the upper watershed for some portions of the year (Figure 7). This leads to average downstream migrants doubling their FL with only a few months of estuary residence. High growth is probably due to the abundance of gammarid amphipods (*Gammarus* sp.) in the estuary, which are a preferred food source of steelhead inhabiting coastal estuaries (Needham 1939). Although only qualitative surveys were performed, gammarids were not observed upstream of the lagoon. Incidentally, fall estuary fish were similar in size to smolts found in more northerly populations (Ward and Slaney 1988; Lohr and Bryant 1999). This may indicate that estuaries in central California are filling a role that upstream waters have in the northern part of the steelhead range.

Although growth rates in the estuary were always higher than the upper watershed, growth in the estuary appears to be density-dependent, with growth rates decreasing as the number of fish utilizing the estuary increases. However, the decrease in growth rates with increasing fish density had little effect on the eventual size of fall estuary fish. This is probably due to annual flow regimes altering the number of days that productive lagoon conditions were available to young steelhead. Therefore, during low flow years when deep-water conditions formed earlier, the population was larger and growth rates were lower, but each fish had a longer period of time to experience that habitat before winter bar breakage allows fish to move to sea. Because of this dynamic, fall estuary fish were very similar in size regardless of sandbar formation date and population size. It is important to note however, that the estuary is currently quite small and the sandbar formation dynamics may be very different since coastal development in the 1930's restricted the Scott Creek estuary to a fraction of its historic size[3]. In fact, the severe alteration of the estuary is probably the largest anthropogenic change to the watershed, as much of the upper watershed remains in an undeveloped state.

Juvenile steelhead growth in the estuary is relatively unaffected by competition for prey by other fish species. Coho salmon are abundant during some years in Scott Creek, but are rarely observed in the estuary, and do not appear to reside there for more than a few weeks. Threespine sticklebacks are often found in abundance in the estuary, although it is unclear how much competition for resources exists between these species.

It is likely that estuary mortality is low in Scott Creek because there appear to be few predators. Unlike many estuaries, no marine mammals have been observed in the Scott Creek estuary. Prickly sculpin have been observed feeding on smaller steelhead in the upper watershed, however most steelhead entering the estuarine water were probably large enough to avoid predation by prickly sculpin. Avian predators

---

[3] California Highway 1, constructed in the late 1930's along the California coast potentially altered the size and seasonal dynamics of estuaries in many watersheds, Scott Creek included, as indicated by historic aerial photographs.

are an important source of mortality for estuarine salmonids, particularly steelhead in the Columbia River estuary, with birds consuming greater than 10% of the steelhead previously detected moving into the estuary (Ryan et al. 2003). Avian predators, while often present, are found in low numbers in the Scott Creek estuary. To a limited extent mergansers have been observed, but they appear to utilize upstream areas with riparian cover more readily than the open estuary habitat. In fact, the deeper estuarine water may provide a refuge from the avian predators (e.g., mergansers, *Mergus* sp.; kingfishers, *Ceryle alcyon*; great blue herons, *Ardea herodias*) that readily feed on steelhead in the shallower upstream waters. Further study is required to determine what effect predation has on the distribution and density of steelhead in the estuary. It is certainly possible though, that steelhead utilize the Scott Creek estuary specifically because of the excellent growth opportunity it provides, and the relatively low predation pressure compared to marine environments. Additionally, small coastal estuaries in central and southern California streams appear to function much differently than larger estuaries (e.g., Columbia River mouth, San Francisco Bay). Many of the larger estuaries have extensive populations of large piscivorous fish (e.g., cutthroat trout, *Oncorhynchus clarki*; striped bass, *Morone saxatilis*), and potentially vast communities of competitors (e.g., other salmonids, *Oncorhynchus* sp.; perch, Percidae; shad, *alosa sapidissima*; smelt, Osmeridae; sole, Soleidae) and extended residence in these areas may not offer the same advantages that smaller estuaries, with few other fish species may provide.

Do estuary reared fish recruit disproportionately to the adult population compared to upstream reared individuals

Scale chemistry

Scale microchemistry indicated that there may be compelling trends in the chemical signatures imparted in calcified structures as an indicator of habitat use. However, there appears to be instability issues in the chemical composition of scales, with potential overwriting of previous chemistry (Figure 11). This may be due to the physiological changes associated with smoltification. Fish do have the capacity to draw upon scales when calcium is needed, and chemical signatures may be lost during that process (Persson et al. 1998; Persson et al. 1999; Kacem et al. 2000). In addition, when estuary sandbar formation occurs, the estuary often becomes mostly freshwater, which may be nearly identical in chemistry to the upstream tributaries. What few pockets of salinity remain during this time become hypoxic, reduced environments over time and are easily avoided by inhabiting steelhead. Although chemical analysis of scales indicated some patterns of interest, more work is needed to establish the potential for long-term stability in anadromous fish.

Size at ocean entry

Back-calculation of size at ocean entry from the morphological characteristics of scales from returning adults indicates that surviving adults were quite large as juveniles at ocean entry. In fact, the vast majority of survivors were so large at ocean entry that the upstream waters alone could not have produced them, as indicated by the size of downstream migrants (Figure 9). Only one returning adult had an ocean entry size (90 mm FL) near the average downstream migrant size (106 mm FL). Fewer than 15% of downstream migrants were above the size threshold (140 mm FL) where the vast majority of returning adults originally went to sea. Additionally, only a small fraction of downstream migrants (<0.01%) captured over 4 years (2002-2005) were larger than 200 mm FL, yet the majority (56%) of returning adults were at least that size upon ocean entry as juveniles. Size-dependent survival in both wild and hatchery fish indicates that small fish are less likely to survive in the marine environment, and estuary-reared juveniles comprise most of the returning adult population.

Scale morphology

Although the relationship between somatic growth and rate of circuli deposition may be somewhat weak, I was able to use the spacing and variance of the spacing to successfully discriminate between estuarine and upstream-reared individuals with 86% accuracy because growth rates are very different in the two habitats. I was then able to assign each returning adult to a freshwater rearing habitat. The vast majority of adult steelhead (~85%) were assigned to rearing in estuary habitat, regardless of their year of return, or year of ocean entry. Habitat assignment by circuli spacing and size at ocean entry give two independent measures of habitat use that both implicate the estuary as having been used by most surviving adult steelhead as juveniles.

PIT tag returns

Some adults returning in the winter and spring of 2004/2005 carried PIT tags from juvenile implantation. Because these fish returned in nearly the same ratio in which estuary fish were tagged (1:10.9 vs. 1:10 respectively) there was probably a large number of untagged estuary-reared fish, which returned as well, which is indicated by the scale circuli spacing data. Because estuary fish were tagged randomly, there is no reason to believe that there was any bias in the return of tagged fish over untagged individuals. Every adult that returned with a PIT tag was either tagged or observed in the estuary during the summer and fall. This is further evidence that migrating steelhead that did not use the estuary experienced very poor survival at sea. I estimated survival rates of estuary-reared juveniles to be 8.3 percent from the 2003 estuary cohort, as compared to the 3.3 percent of the total population from the 2003 cohort. However, no fish tagged at the spring migrant trap that were not observed in the estuary in the summer and fall of 2003 were recaptured as adults, further indicating a weak ocean survival of the 2003 smolt class that did not utilize the estuarine habitat.

CONCLUSIONS

The results of this study support the contention of size-dependent ocean mortality of central California coastal steelhead. Further, these data strongly suggest the estuary as being important nursery habitat for producing large steelhead with increased ocean survival. Estuarine waters in Scott Creek comprise less than 3% of the habitat available to steelhead, yet the vast majority of the adult population may be products of that environment. This indicates that coastal estuaries may be more important to steelhead persistence in the southern portion of their range than previously thought, and their degradation could have drastic implications for steelhead populations already listed as threatened or endangered. Indeed, restoration of coastal estuaries may be an effective method of returning steelhead to their historic population levels in these watersheds. Finally, more work is needed to determine what strategies steelhead take in watersheds without estuaries, to achieve a size large enough to survive at sea without the additional growth these habitats afford. In addition, the strength of size-selective mortality in the ocean appears to be strong enough that the very small size at ocean entry observed in Scott Creek should not persist in the population. More work is needed to determine what conditions may favor the small size at ocean entry and why it is maintained in the face of strong selection against small smolts.

Table 1. Proportion of downstream migrating juvenile steelhead utilizing the estuary in 2003 and 2004.

Year	# of hatchery fish released	# of hatchery fish captured	Estimated % of hatchery fish captured	# of wild downstream migrants captured	Estimated total # of wild downstream migrants	Estuary population ±SD	% of downstream migrants utilizing the estuary
2003	7500	827	11.02	581*	5272*	2540 ±479.4	48
2004	3770	470	12.46	2287	18354	1489 ±381.9	8

* 2003 is assumed to be an underestimate because of the large mesh size of the net used to capture downstream migrants.

Table 2. Mean FL of downstream migrants and late summer estuary residents.

	Downstream Migrants			Estuary Residents	
Year	**Trapping Dates**	**n**	**Mean Fork Length (mm) ±SD**	**Estuary Population ±SD**	**Mean Fork Length at Ocean Entry ± SD**
2002	April-July	370	110.2 ±25	N/A	196.2 ±21
2003	Jan.-July	386	110.0 ±29	2540 ±479	213.6 ±32
2004	Jan.-July	306	92.6 ±24	1489 ±381	182.5 ±26
2005	March-July	113	96.0 ±25	540 ±93	191.1 ±33
All Years		1175	102.2 ±26	1523 ±317	195.8 ±28

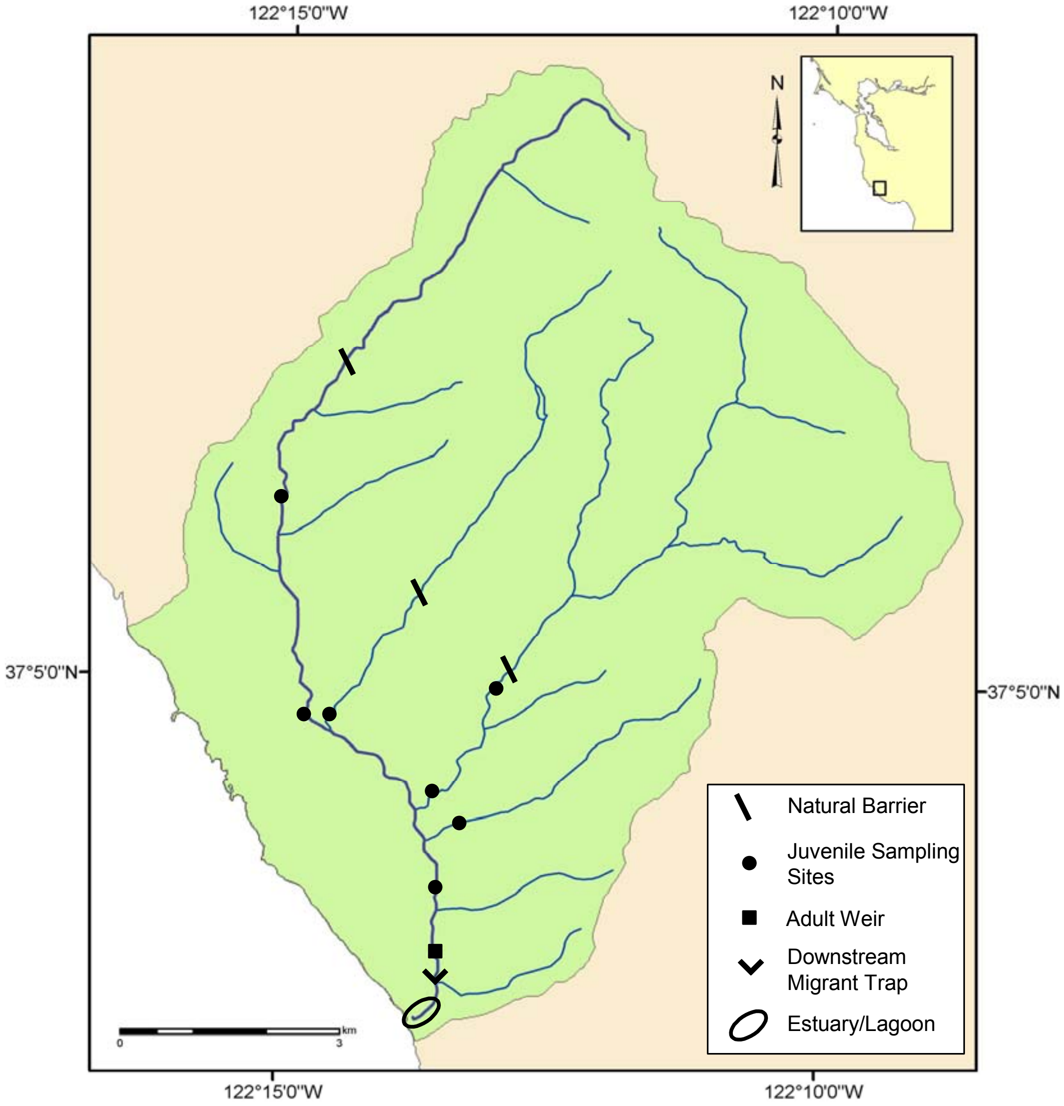


Figure 1. Scott Creek Watershed

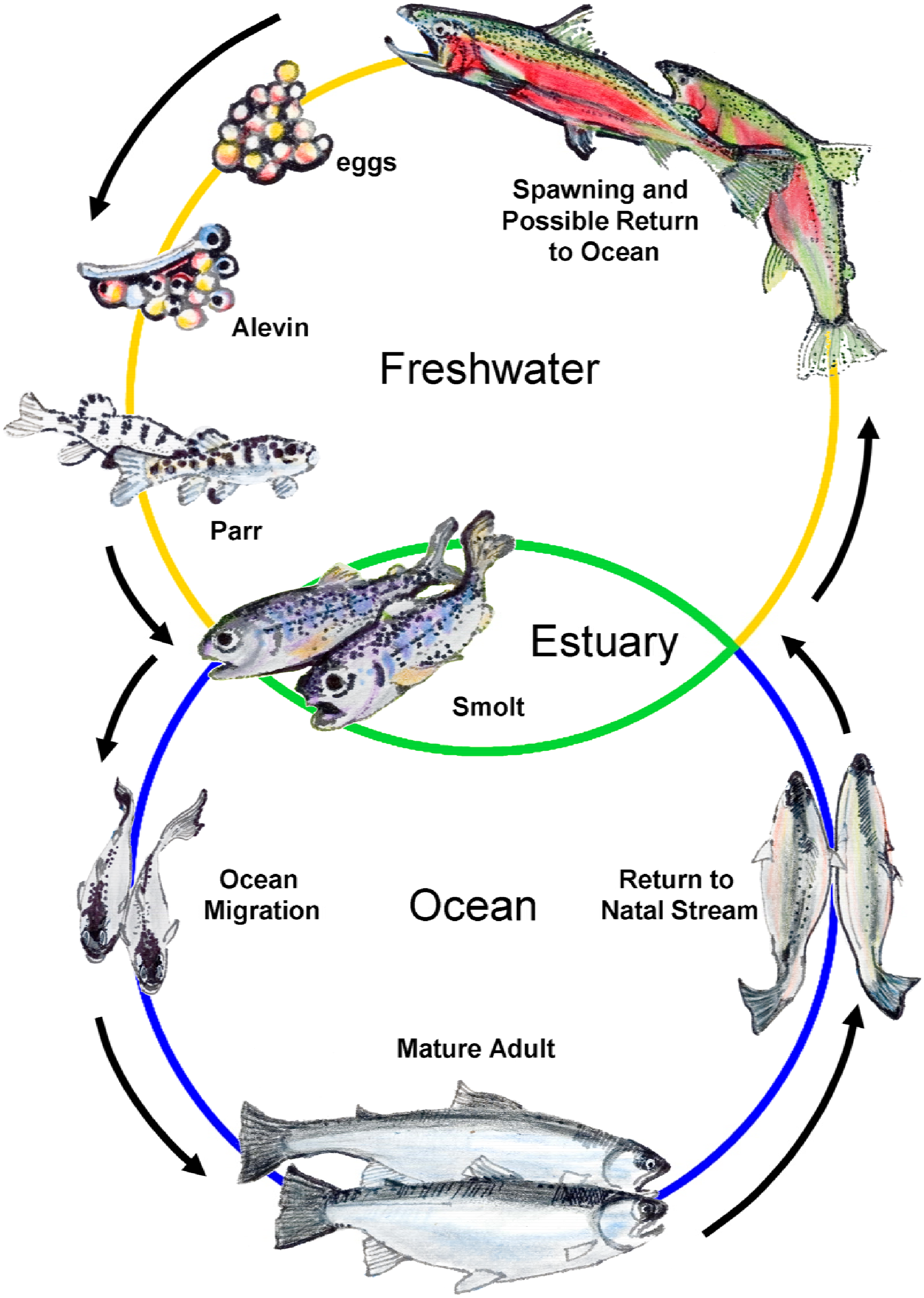


Figure 2. Steelhead Life-Cycle (Drawings by Susan Turner)

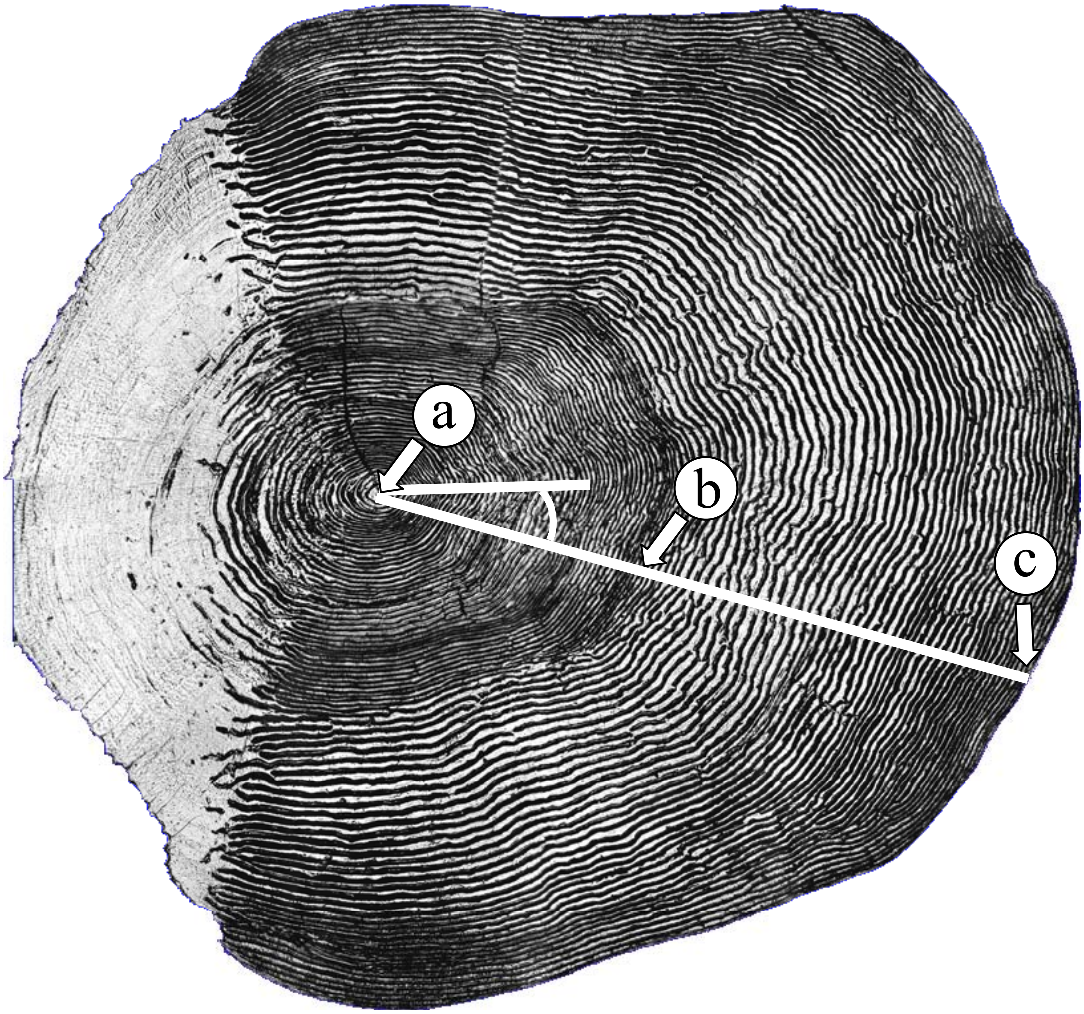


Figure 3. Photograph of scale indicating; a, focus of scale, b, ocean entry radius (OER) and c, scale radius (SR) and the 20° offset from the center axis used to make measurements.

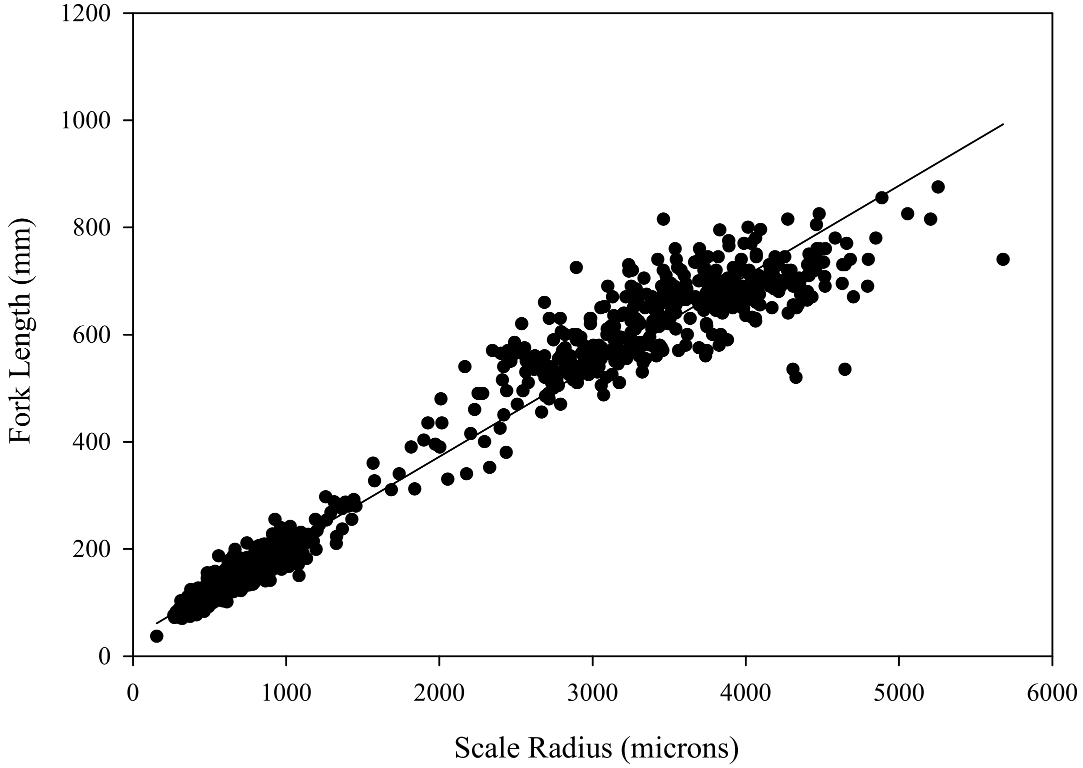


Figure 4. Relationship between fork length and scale radius based on scales from juvenile and adult steelhead collected throughout the watershed n=1250 (2002-2005). FL=0.1686(SR)+34.87 R^2=0.97

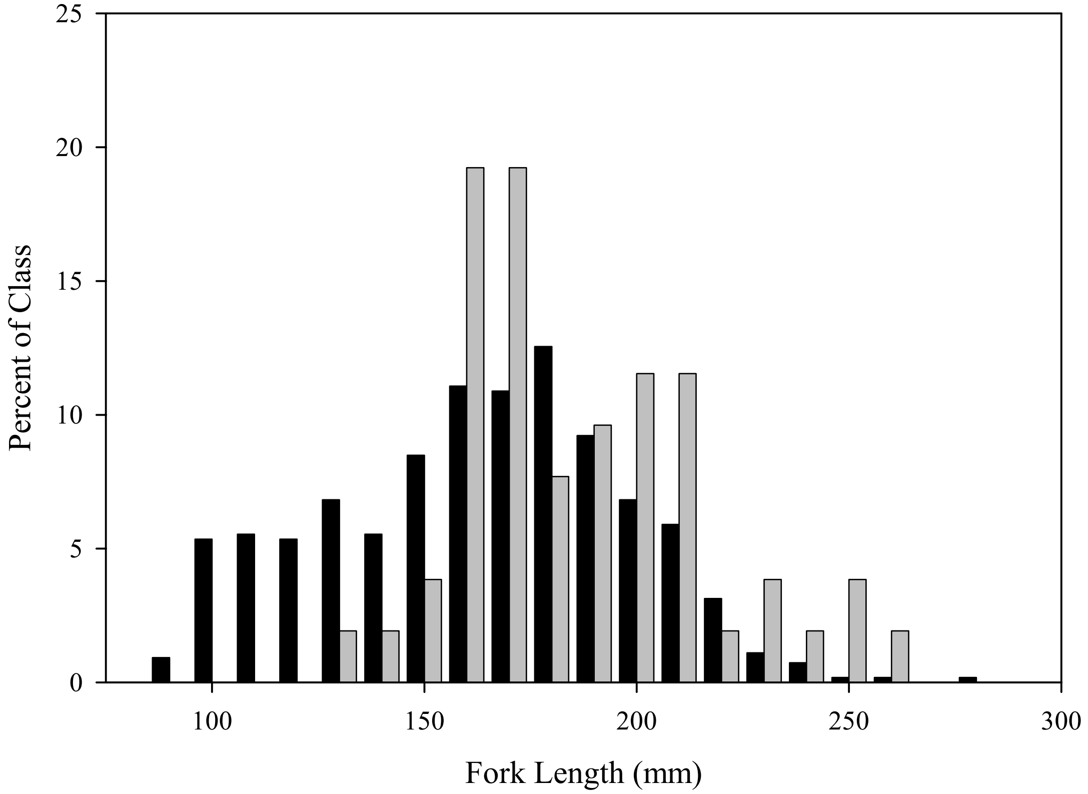


Figure 5. Size distributions of juvenile hatchery smolts (n=542, black bars) sampled immediately preceding release, and the back-calculated size at ocean entry of surviving adults from the same cohort (n=52, grey bars).

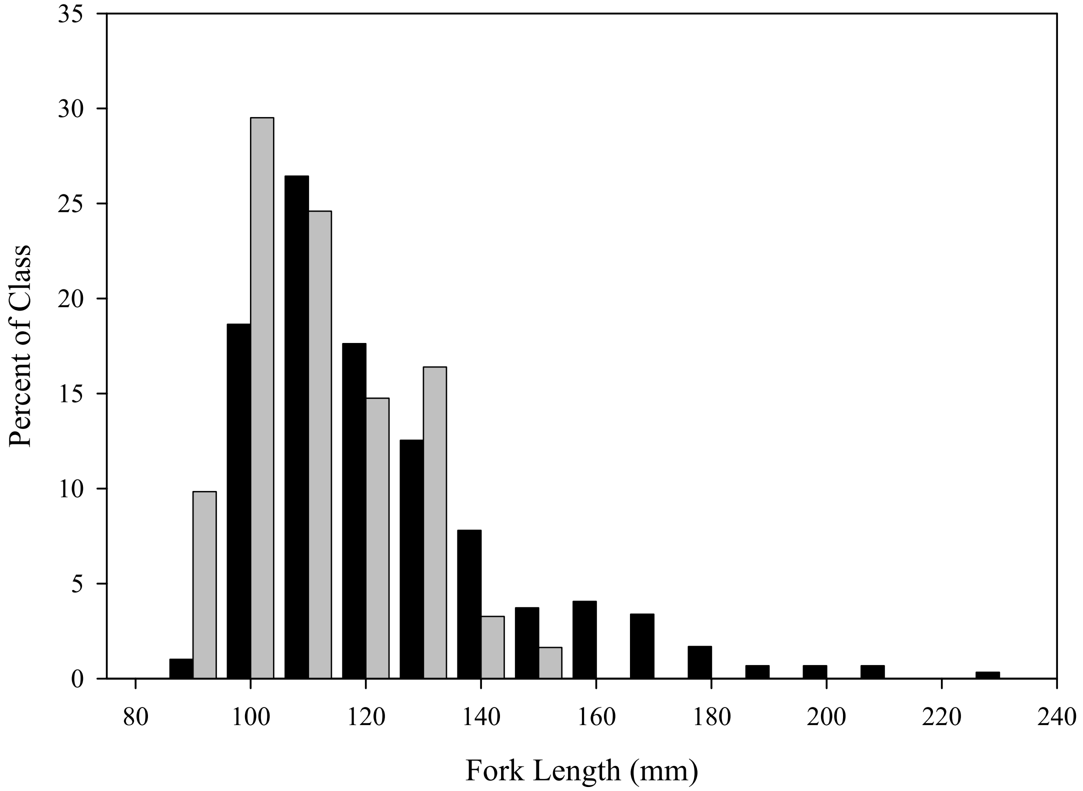


Figure 6. Size distribution of spring downstream migrants PIT tagged prior to estuary entry (n=298, black bars), and the size at initial estuary entry of tagged fish recaptured in the estuary after sandbar closure (n=61, grey bars).

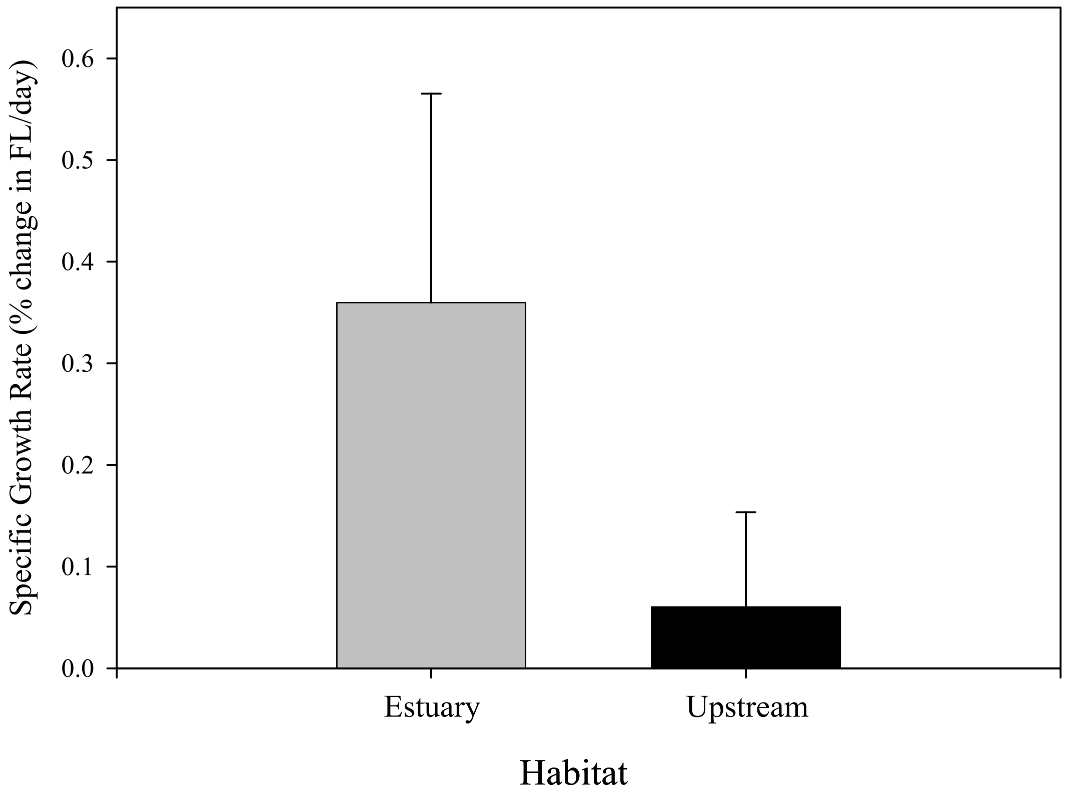


Figure 7. Specific mean (+1 SD) daily growth rates of estuary-reared (grey bar) and upstream (black bar) juvenile steelhead for 2003 and 2004.

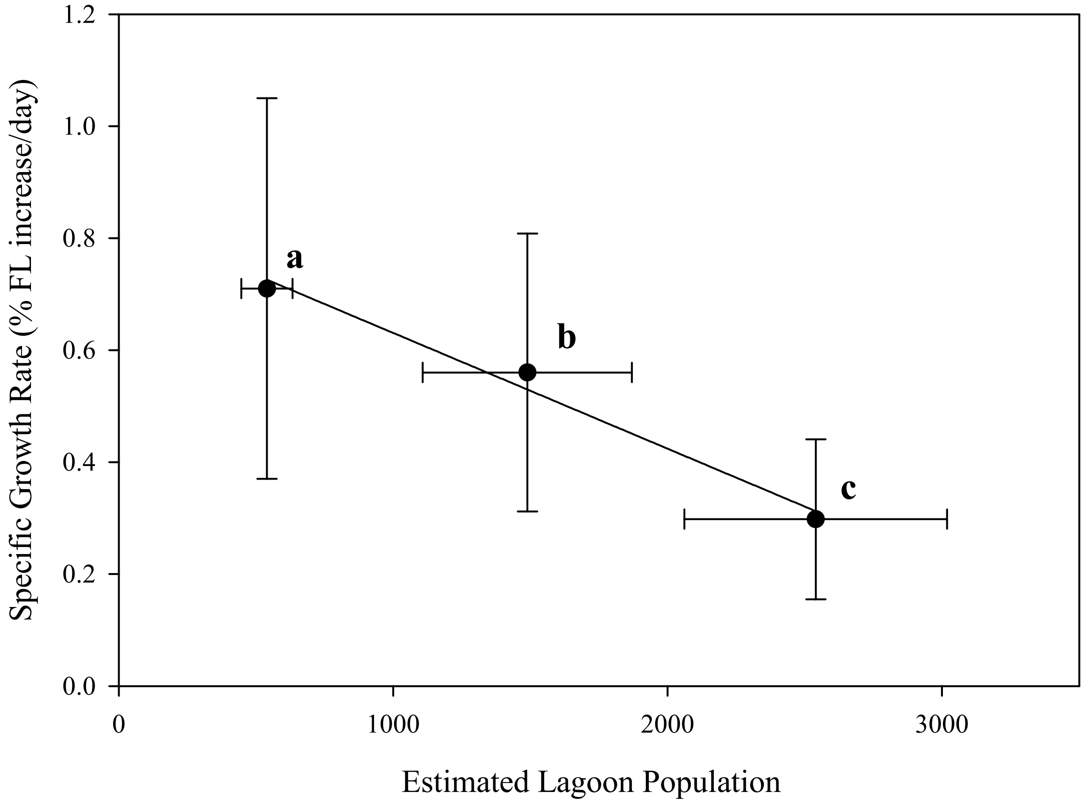


Figure 8. Estimated post-closure estuary population sizes and growth rates from (**a**) 2005, (**b**) 2004, (**c**) 2003. All data are means ±SD. SPGR=-0.000206(Population Size)+0.837 R^2=0.98

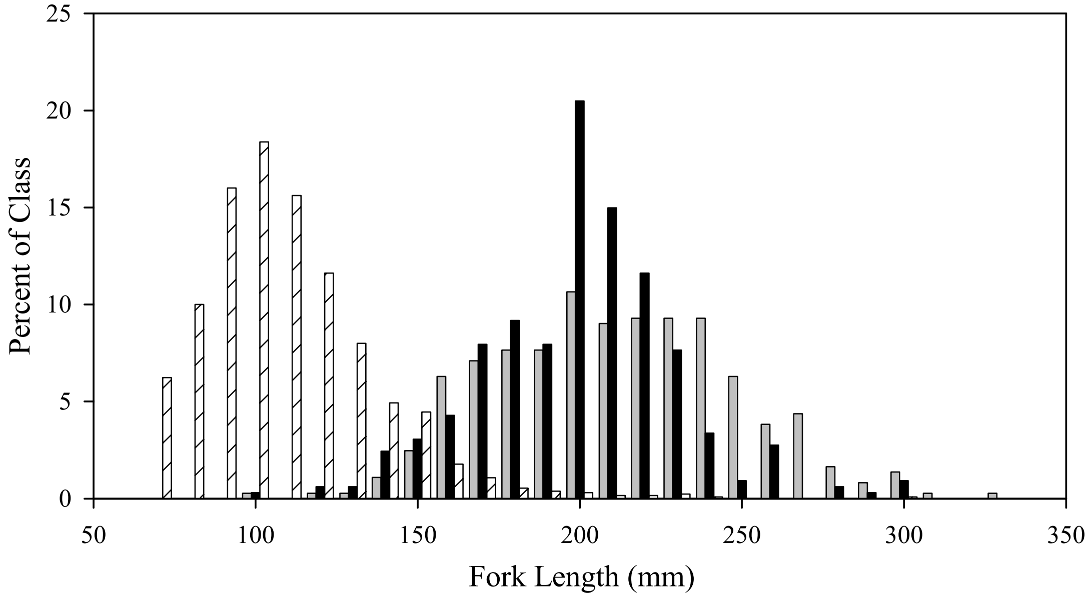


Figure 9. Summed size distribution of all downstream migrants 2002-2004, (n=1300, hashed bars), late fall estuary residents 2002-2005, (n=327, black bars), and back-calculated size at ocean entry of adults returning in 2002-2005, (n=364, grey bars).

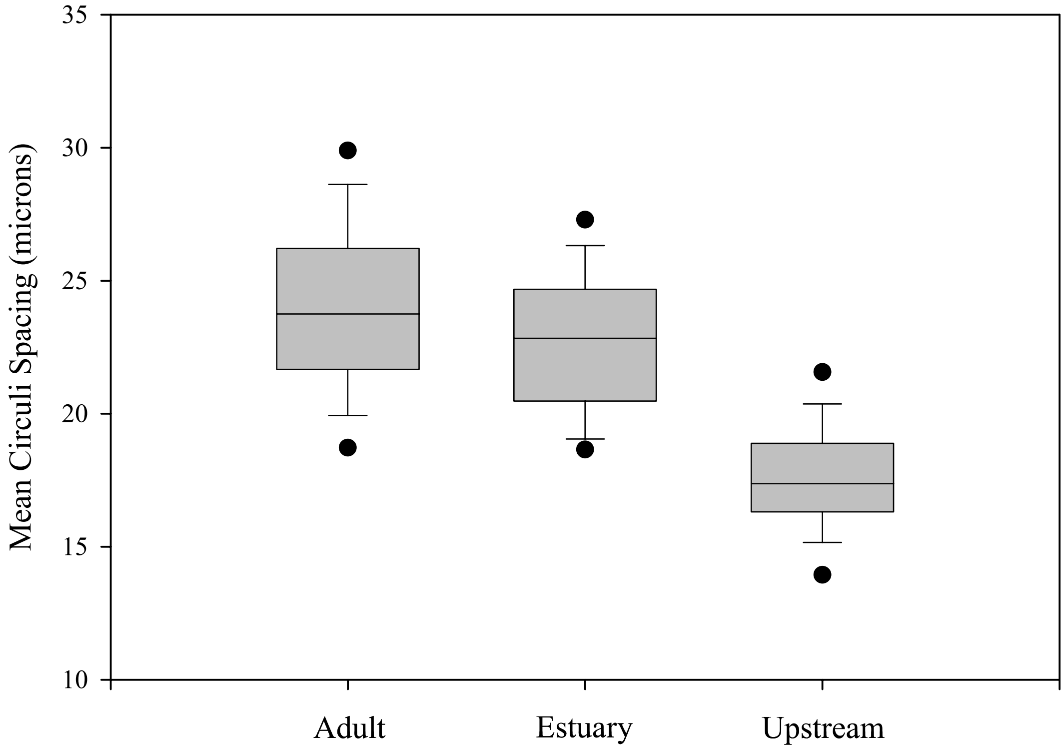


Figure 10. Boxplot depicting the distribution of the mean circuli spacing for the last 18 freshwater circuli for: The freshwater portion of returning adult scales, fall estuary juveniles, and upstream juveniles. Centerline indicates median spacing, while the outer edge of the box indicates the 25th and 75th percentiles. Whiskers indicate 10th and 90th percentiles, and dots indicate 5th and 95th percentiles.

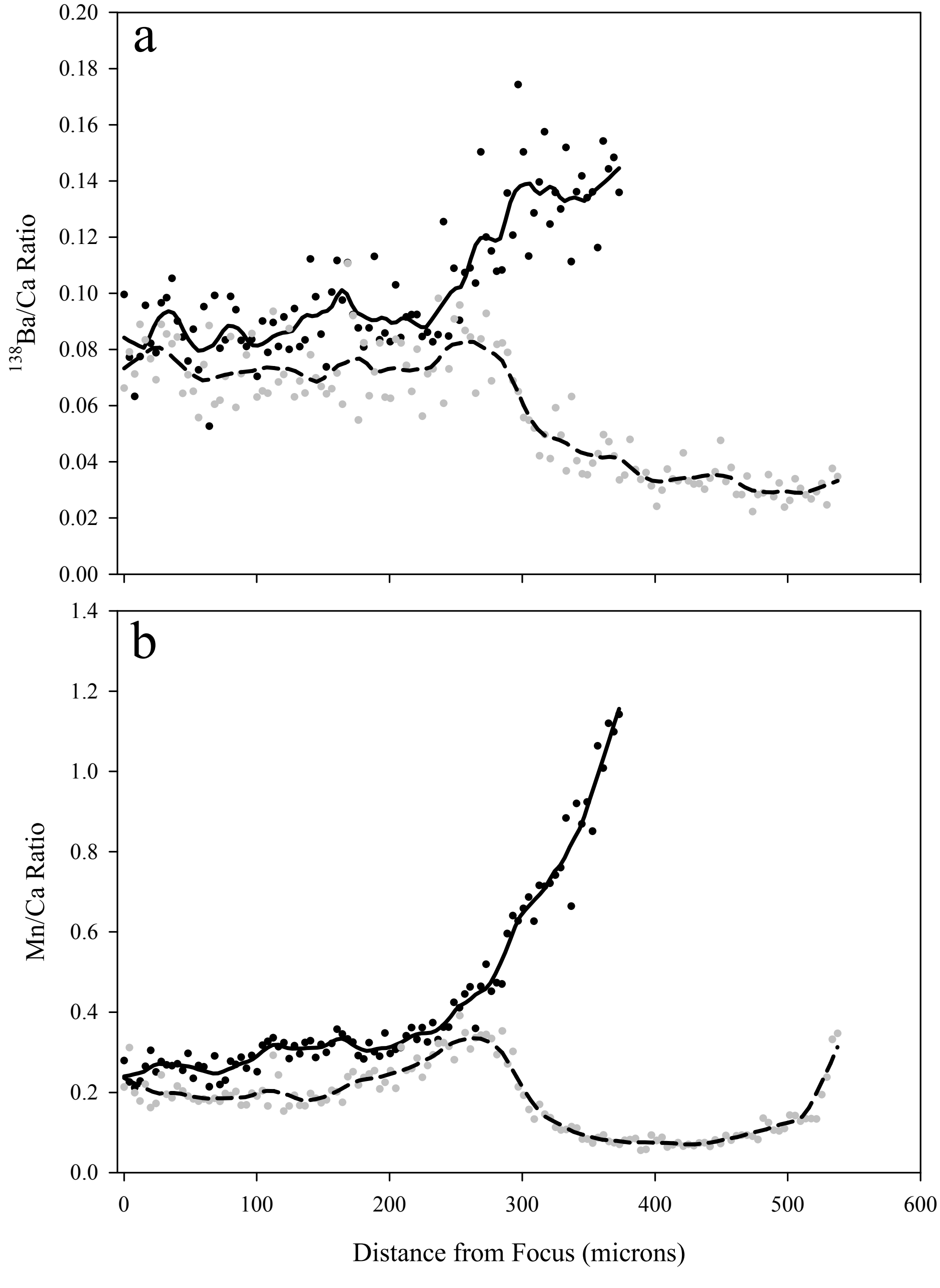


Figure 11. Graphs depicting loess smoothed **(a)** ^{138}Ba:Ca, and **(b)** Mn:Ca ratios from the focus to the margin on a scale from a juvenile steelhead captured at the downstream migrant trap on 6/22/2004 at 78 mm FL (solid black line), and 78 days later in the estuary at 135 mm FL (dashed line). These data are typical of multiple scales analyzed from pre-and post-estuary entrance.

Appendix A. Numbers of hatchery and wild produced steelhead sampled (i.e. measured, tagged or scales taken) over the course of the study.

Year	Upstream Juveniles Tagged and Sampled		Downstream Migrants Sampled		Lagoon Juveniles Sampled		Adults Sampled	
	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery
2002	0	0	455	21	650	8	39	17
2003	270	2	621	10	695	13	51	42
2004	381	2	953	11	473	0	256	104
2005	57	0	235	3	605	3	141	90

REFERENCES

Beck, M. W., K. L. Heck, Jr., K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51(8):633-641.

Bernard, R. L., and K. W. Myers. 1996. The performance of quantitative scale pattern analysis in the identification of hatchery and wild steelhead (Oncorhynchus mykiss). Canadian Journal of Fisheries and Aquatic Sciences 53(8):1727-1735.

Boehlert, G. W., and M. M. Yoklavich. 1983. Effects of Temperature, Ration, and Fish Size on Growth of Juvenile Black Rockfish, Sebastes-Melanops. Environmental Biology of Fishes 8(1):17-28.

Bottom, D. L., K. K. Jones, T. J. Cornwell, A. Gray, and C. A. Simenstad. 2005. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). Estuarine, Coastal and Shelf Science 64:79-93.

Brown, J. A. 2006. Using the chemical composition of otoliths to evaluate the nursery role of estuaries for English sole Pleuronectes vetulus populations. Marine Ecology-Progress Series 306:269-281.

Burgner, R. L., J. T. Light, L. Margolis, T. Okazaki, A. Tautz, and S. Ito. 1992. Distribution and Origins of Steelhead Trout Oncorhynchus-Mykiss in Offshore Waters of the North Pacific Ocean. International North Pacific Fisheries Commission Bulletin (51):1-92.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status Review of West Coast Steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27, NOAA Technical Memorandum NMFS-NWFSC-27.

Davies, P. E., and R. D. Sloane. 1986. Validation of Aging and Length Back-Calculation in Rainbow Trout Salmo-Gairdneri from Dee Lagoon Tasmania Australia. Australian Journal of Marine and Freshwater Research 37(2):289-296.

Dawley, E. M., R. D. Ledgerwood, T. H. Blahm, C. W. Sims, J. T. Durkin, R. A. Kirn, A. E. Rankis, G. E. Monan, and F. J. Ossiander. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966-1983. Final Report to the Bonneville Power Administration, Project 81-102, Portland, Oregon.

Dawley, E. M., R. D. Ledgerwood, and A. L. Jensen. 1985. Beach and Purse Seine Sampling of Juvenile Salmonids in the Columbia River Estuary and Ocean Plume, 1977-1983. NMFS, NMFS F/NWC-75, Seattle, WA.

Epifanio, C. E., A. I. Dittel, R. a. Rodriguez, and T. E. Targett. 2003. The role of macroalgal beds as nursery habitat for juvenile blue crabs, Callinectes sapidus. Journal of Shellfish Research 22(3):881-886.

Fisher, J. P., and W. G. Pearcy. 1990. Spacing of Scale Circuli Versus Growth-Rate in Young Coho Salmon. Fishery Bulletin 88(4):637-643.

Fisher, J. P., and W. G. Pearcy. 2005. Seasonal changes in growth of coho salmon (Oncorhynchus kisutch) off Oregon and Washington and concurrent changes in the spacing of scale circuli. Fishery Bulletin 103(1):34-51.

Francis, R. I. C. C. 1990. Back-Calculation of Fish Length a Critical Review. Journal of Fish Biology 36(6):883-902.

Fraser, C. M. 1916. Growth of the spring salmon. Transactions of the Pacific Fisheries Society 7(6):5-8.

Fukuwaka, M. A., and M. Kaeriyama. 1997. Scale analyses to estimate somatic growth in sockeye salmon, Oncorhynchus nerka. Canadian Journal of Fisheries and Aquatic Sciences 54(3):631-636.

Gregory, R. S. 1993. Effect of Turbidity on the Predator Avoidance-Behavior of Juvenile Chinook Salmon (Oncorhynchus-Tshawytscha). Canadian Journal of Fisheries and Aquatic Sciences 50(2):241-246.

Handeland, S. O., and S. O. Stefansson. 2001. Photoperiod control and influence of body size on off-season parr-smolt transformation and post-smolt growth. Aquaculture 192(2-4):291-307.

Harvey, B. C., J. L. White, and R. J. Nakamoto. 2005. Habitat-specific biomass, survival, and growth of rainbow trout (Oncorhynchus mykiss) during summer in a small coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 62(3):650-658.

Hayes, S. A., M. H. Bond, C. V. Hanson, and R. B. MacFarlane. 2004. Interactions between endangered wild and hatchery salmonids: can the pitfalls of artificial propagation be avoided in small coastal streams? Journal of Fish Biology 65:101-121.

Healey, M. C. 1991. Life History of Chinook Salmon Oncorhynchus-Tshawytscha. Pages 313-394 *in* C. A. L. M. Groot, editor. Pacific Salmon Life Histories. University of British Columbia: Vancouver, British Columbia.

Hoar, W. S. 1976. Smolt Transformation - Evolution, Behavior, and Physiology. Journal of the Fisheries Research Board of Canada 33(5):1233-1252.

Hoplain, J. S. 1998. Age, Growth, And Life History of Klamath River Basin Steelhead Trout (Oncorhynchus mykiss irideus) as Determined From Scale Analysis. Inland Fisheries Division Administrative Report No. 98-3 98-3.

Iwata, M., and S. Komatsu. 1984. Importance of Estuarine Residence for Adaptation of Chum Salmon Oncorhynchus-Keta Fry to Sea Water. Canadian Journal of Fisheries and Aquatic Sciences 41(5):744-749.

Jonsson, N., B. Jonsson, and L. F. Hansen. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. Journal of Applied Ecology 40(5):900-911.

Kacem, A., S. Gustafsson, and F. J. Meunier. 2000. Demineralization of the vertebral skeleton in Atlantic salmon Salmo salar L. during spawning migration. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 125(4):479-484.

Kesner, W. D., and R. A. Barnhart. 1972. Characteristics of the fall-run steelhead trout (Salmo gairdneri gairdneri) of the Klamath River system with emphasis on the half-pounder. California Fish and Game 58(3):204-220.

Klumb, R. A., M. A. Bozek, and R. V. Frie. 1999. Proportionality of body to scale growth: Validation of two back-calculation models with individually tagged and recaptured smallmouth bass and walleyes. Transactions of the American Fisheries Society 128(5):815-831.

Le Pape, O., F. Chauvet, Y. Desaunay, and D. Guerault. 2003. Relationship between interannual variations of the river plume and the extent of nursery grounds for the common sole (Solea solea, L.) in Vilaine Bay. Effects on recruitment variability. Journal of Sea Research 50(2-3):177-185.

Lee, R. M. 1920. A review of the methods of age and growth determination in fishes by means of scales. Fishery Investigations, Series II, Marine Fisheries, Great Britan Ministry of Agriculture, Fisheries and Food 4(2).

Levy, D. A., and T. G. Northcote. 1982. Juvenile Salmon Residency in a Marsh Area of the Fraser River Estuary Canada. Canadian Journal of Fisheries & Aquatic Sciences 39(2):270-276.

Lohr, S. C., and M. D. Bryant. 1999. Biological characteristics and population status of steelhead (Oncorhynchus mykiss) in southeast Alaska. U S Forest Service General Technical Report PNW 0(407):1-20.

Macdonald, J. S., I. K. Birtwell, and G. M. Kruzynski. 1987. Food and Habitat Utilization by Juvenile Salmonids in the Campbell River Estuary Vancouver Canada. Canadian Journal of Fisheries and Aquatic Sciences 44(6):1233-1246.

MacFarlane, R. B., and E. C. Norton. 2002. Physiological ecology of juvenile chinook salmon (Oncorhynchus tshawytscha) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fishery Bulletin 100(2):244-257.

Maher, F. P., and P. A. Larkin. 1954. Life History of the steelhead trout of the Chilliwack river, B.C. Transactions of the American Fisheries Society 84:27-38.

McCabe, G. T., R. L. Emmett, W. D. Muir, and T. H. Blahm. 1986. Utilization of the Columbia River Estuary by Subyearling Chinook Salmon. Northwest Science 60(2):113-124.

Miller, B. A., and S. Sadro. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. Transactions of the American Fisheries Society 132(3):546-559.

Mitro, M. G., and A. V. Zale. 2002. Seasonal survival, movement, and habitat use of age-0 rainbow trout in the Henrys Fork of the Snake River, Idaho. Transactions of the American Fisheries Society 131(2):271-286.

Myers, K. W., and H. F. Horton. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. V. S. Kennedy, editor. Estuarine Comparisons. Academic Press, New York.

Myrick, C. A., and J. J. Cech. 2004. Temperature effects on juvenile anadromous salmonids in California's central valley: what don't we know? Reviews in Fish Biology and Fisheries 14(1):113-123.

Needham, P. R. 1939. Quantitative and qualitative observations on fish foods in Waddell Creek Lagoon. Transactions of the American Fisheries Society vol. 69:p. 178-186.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: Stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4-21.

Panfili, J., and H. Troadec. 2002. Manual of fish sclerochronology. Ifremer, Plouzanâe, France.

Persson, P., B. T. Bjornsson, and Y. Takagi. 1999. Characterization of morphology and physiological actions of scale osteoclasts in the rainbow trout. Journal of Fish Biology 54(3):669-684.

Persson, P., K. Sundell, B. T. Bjornsson, and H. Lundqvist. 1998. Calcium metabolism and osmoregulation during sexual maturation of river running Atlantic salmon. Journal of Fish Biology 52(2):334-349.

Quinones, R. M., and T. J. Mulligan. 2005. Habitat use by juvenile salmonids in the Smith River estuary, California. Transactions of the American Fisheries Society 134(5):1147-1158.

Reimers, P. E. 1973. The Length of Residence of Juvenile Fall Chinook Salmon in Sixes river, Oregon. Research Reports of the Fish Commission of Oregon 4(2):1-43.

Ricker, W. E. 1992. Back-Calculation of Fish Lengths Based on Proportionality between Scale and Length Increments. Canadian Journal of Fisheries & Aquatic Sciences 49(5):1018-1026.

Roff, D. A. 1973. On the accuracy of some mark-recapture estimators. Oecologia 12(1):15-34.

Ryan, B. A., S. G. Smith, J. M. Butzerin, and J. W. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary, 1998-2000. Transactions of the American Fisheries Society 132(2):275-288.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*). California Department of Fish and Game, Fish Bulletin 98:375pp.

Shreffler, D. K., C. A. Simenstad, and R. M. Thom. 1992. Foraging by Juvenile Salmon in a Restored Estuarine Wetland. Estuaries 15(2):204-213.

Simenstad, C. A., K. L. Fresh, and E. O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of pacific salmon: an unappreciated function. V. S. Kennedy, editor. Estuarine Comparisons. Academic Press, New York.

Snyder, C. O. 1938. A study of the trout (*Salmo irideus* Gibbons) from Waddell Creek, California. California Department of Fish and Game 24(4):354-375.

Sogard, S. M. 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. Marine Ecology Progress Series 85(1-2):35-53.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bulletin of Marine Science 60(3):1129-1157.

Tattam, I. A., T. A. Whitesel, and Y. Pan. 2003. Scale Pattern Analysis of Selected Scale Characteristics and the First Annulus for Distinguishing Wild and Hatchery Steelhead in the Hood River, Oregon. North American Journal of Fisheries Management 23(3):856-868.

Thorpe, J. E. 1994. Salmonid Fishes and the Estuarine Environment. Estuaries 17(1A):76-93.

Tobin, J. H. 1994. Construction and performance of a portable resistance board weir for counting adult salmon in rivers. US Department of Fish and Wildlife, 22, Kenai, Alaska.

Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 45(7):1110-1122.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): Back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46(11):1853-1858.

Wells, B. K., B. E. Rieman, J. L. Clayton, D. L. Horan, and C. M. Jones. 2003. Relationships between water, otolith, and scale chemistries of westslope cutthroat trout from the Coeur d'Alene River, Idaho: The potential application of hard-part chemistry to describe movements in freshwater. Transactions of the American Fisheries Society 132(3):409-424.

Yamashita, Y., T. Otake, and H. Yamada. 2000. Relative contributions from exposed inshore and estuarine nursery grounds to the recruitment of stone flounder, Platichthys bicoloratus, estimated using otolith Sr:Ca ratios. Fisheries Oceanography 9(4):316-327.

Zaugg, W. S., and H. H. Wagner. 1973. Gill Atpase Activity Related to Parr Smolt Transformation and Migration in Steelhead Trout Salmo-Gairdneri Influence of Photoperiod and Temperature. Comparative Biochemistry & Physiology B 45(4):955-965.

Transactions of the American Fisheries Society 137:114–128, 2008
© Copyright by the American Fisheries Society 2008
DOI: 10.1577/T07-043.1

[Article]

Steelhead Growth in a Small Central California Watershed: Upstream and Estuarine Rearing Patterns

Sean A. Hayes,* Morgan H. Bond, Chad V. Hanson, and Ellen V. Freund

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Fisheries Ecology Division, Southwest Fisheries Science Center,
110 Shaffer Road, Santa Cruz, California 95060, USA

Jerry. J. Smith

Department of Biological Sciences, San Jose State University,
1 Washington Square, San Jose, California 95192, USA

Eric C. Anderson, Arnold J. Ammann, and R. Bruce MacFarlane

National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Fisheries Ecology Division, Southwest Fisheries Science Center,
110 Shaffer Road, Santa Cruz, California 95060, USA

Abstract.—We monitored growth and life history pathways of juvenile steelhead *Oncorhynchus mykiss* and compared growth rates between the upper watershed and estuary in Scott Creek, a typical California coastal stream. Growth in the upper watershed was approximately linear from May to December for age-0 fish. For passive integrated transponder (PIT) tagged, age-1+ fish, growth transitioned to a cyclic pattern, peaking at 0.2% per day during February–April, when maximum flows and temperatures of 7–12°C occurred. Growth of PIT-tagged fish then slowed during August–September (0.01% per day), when temperatures were 14–18°C and flows were low. During each spring, smolts (mean fork length [FL] ± SE = 98.0 ± 1.2 mm) and fry migrated to the estuary; some fish remained there during summer–fall as low flows and waves resulted in seasonal sandbar formation, which created a warm lagoon and restricted access to the ocean. Growth in the estuary–lagoon was much higher (0.2–0.8% per day at 15–24°C). Our data suggest the existence of three juvenile life history pathways: upper-watershed rearing, estuary–lagoon rearing, and combined upper-watershed and estuary–lagoon rearing. We present a model based upon the above data that reports size at age for each juvenile life history type. The majority of fish reaching typical steelhead ocean entry sizes (~150–250 mm FL; age 0.8–3.0) were estuary–lagoon reared, which indicates a disproportionate contribution of this habitat type to survival of Scott Creek steelhead. In contrast, steelhead from higher latitudes rear in tributaries during summer, taking several years to attain ocean entry size.

Growth rates, associated environmental influences, and subsequent effects on life history decisions have been extensively studied in Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* in both the laboratory and the field by means of classical periodic sampling and more recently passive integrated transponder (PIT) tag recaptures (e.g., Elliott 1975; Thorpe 1977; Jones and Hutchings 2001; Jones et al. 2002; Arnekleiv et al. 2006;). Comparatively little data exist for Pacific salmonids in the field, and most work is limited to studies of coho salmon *Oncorhynchus kisutch* (Parker and Larkin 1959; Breuser 1961; Chapman 1962; Bustard and Narver 1975; Fransen et al. 1993; Peterson et al. 1994; Bilby et al. 1996). Because Pacific salmon populations exist across broad latitudinal ranges (reviewed in Quinn 2005), it is likely that juvenile growth and life histories vary in response to environmental differences and may have subsequent effects on marine survival and ultimately adult returns. Variation in juvenile growth and life history among populations of steelhead *O. mykiss* is typically evaluated in terms of size and age at ocean entry, measured either directly from smolts or more often estimated from analyses of scales from returning adults (Busby et al. 1996). It is suspected that the amount of time required to reach the size threshold for marine survival depends upon the length of the summer growing season and may take several years in northern latitudes (Withler 1966; Narver 1969; Narver and Andersen 1974; Busby et al. 1996). However, only limited data exist on year-round growth or habitat use for juvenile steelhead across their range, 34–60°N (Hartman 1965).

Environmental conditions may affect seasonal patterns of growth in ways that are not understood,

---

* Corresponding author: sean.hayes@noaa.gov

Received February 26, 2007; accepted July 29, 2007

possibly having both positive and negative effects in the southern part of the steelhead range where many populations are listed under the Endangered Species Act as endangered or threatened (NMFS 2006). Steelhead growth rate varies across temperature and probably among populations, but optimal growth is thought to occur between 15°C and 19°C and lethal temperatures are between 27.5°C and 29.6°C for one southern population (Wurtsbaugh and Davis 1977b; Railsback and Rose 1999; Myrick and Cech 2005). While little is known about steelhead growth in the wild, the longer growing season associated with mild climates at the southern portion of their range may enable the fish to reach smolt stage within a shorter period of time (Withler 1966; Busby et al. 1996). Connolly and Peterson (2003) proposed that overwintering survival might be especially tenuous for larger age-0 steelhead in warmer climates due to the "challenges" of the winter climate—specifically, elevated metabolic rate and limited food. Alternatively, winter conditions may be superior, potentially providing better growing conditions than those in northern-latitude streams due to mild temperatures and better food production. The real challenges faced by southern populations may be associated with summer, when warm temperatures may increase metabolic rates while extremely low flows result in reduced aquatic invertebrate production and terrestrial insect drift in upper watersheds. In fact, growth conditions for some southern populations have been reported as poor during summer and fall, causing scale annulus formation in September (Shapovalov and Taft 1954; Railsback and Rose 1999).

While estuarine use has been studied within the central and northern portions of Pacific salmonid ranges (e.g., Healey 1982; Levings et al. 1986; Tschaplinski 1987; Miller and Sadro 2003; Bottom et al. 2005), limited research exists on the use of coastal estuaries by southern salmonids and the associated effects on growth. Many coastal California streams have estuaries that lose surface connectivity with the ocean during the summer months, forming lagoons (Shapovalov and Taft 1954; Schwarz and Orme 2005). Temperatures in these estuaries and lagoons can range from 15°C to 24°C or more during summer months. Juvenile steelhead are known to use these estuaries, but the effects of estuarine rearing on steelhead growth and survival have been reported only rarely in peer-reviewed literature (e.g., Smith 1990; Cannata 1998).

In this study, we report growth rates of juvenile steelhead from emergence to ocean entry in a typical small stream along the central California coast and we provide a comparative analysis of upstream and estuarine rearing by similarly aged fish. From these results, we describe the associated habitat use patterns and construct growth models for the various life history paths followed by fish before reaching the ocean. Finally, we address how the southern environmental conditions affect steelhead growth and compare our results with the limited growth data available from the remainder of the species' range.

Study Area

Scott Creek is a small, 70-km^2 coastal watershed located 100 km south of San Francisco in central California. Anadromous fish can access approximately 23 km of stream between the estuary and natural upstream barriers of the main stem and the three main tributaries, Little, Big, and Mill creeks (Figure 1). The upper portion of the watershed consists of high-gradient stream dominated by a thick canopy of coastal redwoods *Sequoia sempervirens*. The main stem below the major tributary confluences tends to be characterized by a low gradient, a lower density overstory cover primarily produced by alders *Alnus* spp., and an understory dominated by willows *Salix* spp. A small estuary at the bottom of the watershed can become a freshwater lagoon during summer and fall when a sandbar builds up at the creek mouth, isolating the stream from the ocean. During the last two decades, natural and anthropogenic influences often interfered with lagoon formation (e.g., artificial breaching, water diversions, and drought; J.J.S., unpublished data). Stream width varies from approximately 40 m in the estuary when closed to about 10 m on the main stem, to less than 1 m in the upper tributaries. While the lagoon area and depth varied during the course of this study, measurements made in November 2003 at a typical size indicated an approximate surface area of 18,435 m^2, mean depth of 0.72 m, and a maximum depth of 2.1 m.

Methods

Environmental measurements.—Flows were measured on a cross section of the main stem downstream of major tributaries with a portable flowmeter (Marsh-McBirney, Inc., Frederick, Maryland; Model 2000 Flo-Mate). It was not possible to enter the stream at high-flow events ($>\sim 8$ m^3/s), and flows were estimated from cross-sectional area measurements of peak flow and approximated velocity measurements after flow subsided. Water temperatures were measured on an hourly basis upstream and at the estuary (Figure 1); we initially used IB-Cod temperature loggers (Alpha Mach, Mont St. Hilaire, Quebec; May 2002–June 2003) at both sites and then switched to Onset Tidbits (Onset Computer Corp., Pocasset, Massachusetts) in the upper watershed and YSI 600 XLM data loggers

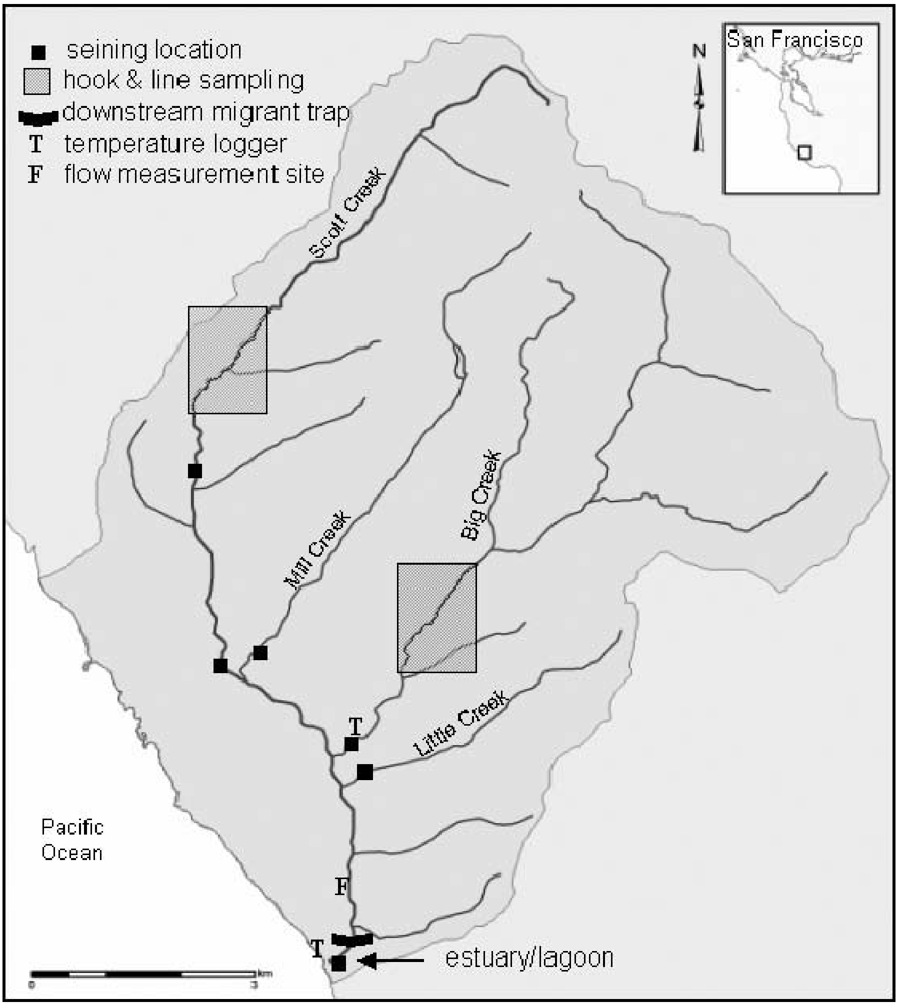


FIGURE 1.—Map of the Scott Creek watershed, California, showing locations where juvenile steelhead were sampled for a study of growth and rearing patterns.

(YSI, Inc., Yellow Springs, Ohio) in the estuary (July 2003–January 2005).

Fish sampling.—Sampling involved multiple methods and age-classes and was conducted in the upper watershed and estuary during May 2002 through November 2006. Specific time frames and methods are summarized in Table 1. Fish were sampled monthly at multiple locations throughout the upper watershed in pools with a 3.0 × 1.5-m beach seine (0.32-cm square mesh) and by hook and line (Figure 1). Downstream-

TABLE 1.—Summary of sampling effort used to determine growth and life history patterns in Scott Creek, California, juvenile steelhead, by age-class, location, tag type applied, collection method, and date range.

Age	Location	Tag type	Collection method	Date range
0	Upper watershed		Seine	May 2002–Dec 2004
0	Upper watershed	Elastomer	Seine	Jun 2003–Dec 2003
1+	Upper watershed	PIT	Seine, hook and line	May 2003–Oct 2004
All	Upper watershed		Electrofisher	Oct 2002–2004
All	Estuary	PIT	Seine	May 2003–Nov 2006
1+	Head of estuary	PIT	Hoop net (smolt trap)	Jan 2003–Nov 2005

migrating fish were trapped at the head of the estuary by means of a two-chambered hoop net (0.635-cm square mesh) with wings extending to each bank. The trap was operated 3 d/week throughout the year except during exceptionally high flows associated with winter storms. Fish in the estuary (downstream of the migrant trap) were captured with a 30 × 2-m beach seine (wings: 0.950-cm square mesh; bag: 0.635-cm square mesh).

Fish were handled according to the methods of Hayes et al. (2004). Specific details for this study are as follows. Up to 20 age-0 fish were randomly sampled for fork length (FL) and mass measurements at each seining site in the upper watershed. To determine whether (1) age-0 fish were remaining at the sample sites and (2) our assessments of age-0 growth by repeated sampling of untagged fish was accurate, we injected 200 age-0 steelhead (between 25 and 65 mm FL) with an elastomer dye (Northwest Marine Technology, Shaw Island, Washington) that was color coded to indicate 5-mm-FL bins. Elastomer injections took place during the second week of June 2003. All fish collected in the upper watershed that exceeded 65 mm FL received a PIT tag (Allflex, Boulder, Colorado; FDX-B Glass Transponder, 11.5 mm) injected intraperitoneally with a 12-gauge needle and were scanned for previously implanted PIT tags. Scale samples were taken from every PIT-tagged fish just posterior and ventral to the dorsal fin on the left side. The PIT tags were also implanted in fish caught at the downstream migrant trap and in the estuary. All collected fish were scanned for previously implanted PIT tags. A subset of untagged fish was sampled and tagged during each collection effort. All recaptured tagged fish were measured for FL and mass, and additional scale samples were taken from the right side of the fish.

In addition to our sampling efforts, relative abundance of juvenile fish was assessed each fall by one of us (J.J.S., unpublished data). Briefly, 12–14 reaches were blocked off and sampled with two passes of a backpack electrofisher (Smith-Root, Inc., Vancouver, Washington; Type 7, smooth pulse) to estimate the number of steelhead and coho salmon per unit length of stream.

Scale analysis.—Scales were flattened between two microscope slides and digitally photographed. Scale images were then analyzed using OPTIMAS software (Media Cybernetics, Silver Springs, Maryland) to measure scale radius, number and location of annuli, and number and distance between circuli. Where age information is reported in the text, a "+" sign is used to indicate all year-classes equal to or greater than the number given (e.g., age 1+).

Growth rate.—Fork lengths of age-0 fish (newly hatched fry to parr stage) were measured repeatedly at five upstream locations on a monthly basis. Growth rates were calculated by determining the temporal change in mean FL. Specific growth rate (SGR) could not be calculated for this size-class, since the calculation is most accurately done with repeated measures on known individuals and age-0 fish were too small to mark with unique identifiers such as PIT tags. During the late summer and fall months, fast-growing age-0 fish began to overlap in size with some age-1 fish. Scale analysis was used to distinguish between individuals in their first and second year. The general linear models (GLM) procedure in SYSTAT version 11 was used to test for significant differences in growth rate among different cohorts of age-0 steelhead and between elastomer-tagged and untagged age-0 steelhead. Hereafter, all means are reported with SEs.

For fish greater than 65 mm FL, SGR in mass and FL was calculated (Busacker et al. 1990) based upon the measured changes in mass and FL of recaptured – PIT-tagged individuals. Growth rate was then applied to the date intermediate between capture events. Only recaptures obtained 7–120 d after the previous capture were used in the analysis. Fish sampled in the upstream habitat were analyzed separately from those in the estuary. Growth rates between habitats and seasons were tested using analysis of variance (ANOVA) in SYSTAT 11. Only one recapture event per individual was used, and all recaptures between upstream and estuarine habitats were excluded.

Estuarine population size was estimated each year (2002–2005) with PIT tags and the Petersen mark–recapture method. After sandbar closure, we tagged a subset of the fish caught in the newly formed lagoon. Seining surveys were repeated each month until winter rains made seining of the estuary impossible. Population size and variance for each month after the initial survey was estimated using equations 3.5 and 3.6, respectively, from Ricker (1975).

It was not possible to quantify mortality due to handling and predation between seining efforts, and we assumed mortality of tagged and untagged fish was equal. In years when multiple samplings were done, estimates were pooled and mean values were used. Mark–recapture methods were not used to estimate population size before sandbar closure because of the possibility of individuals entering the ocean and leaving the population during that time. In addition, the rate of downstream migration drops rapidly after June and we assumed addition of new migrants to be negligible (Hayes et al. 2004). There may have been some movement from the estuary back upstream, which would result in an overestimation of the

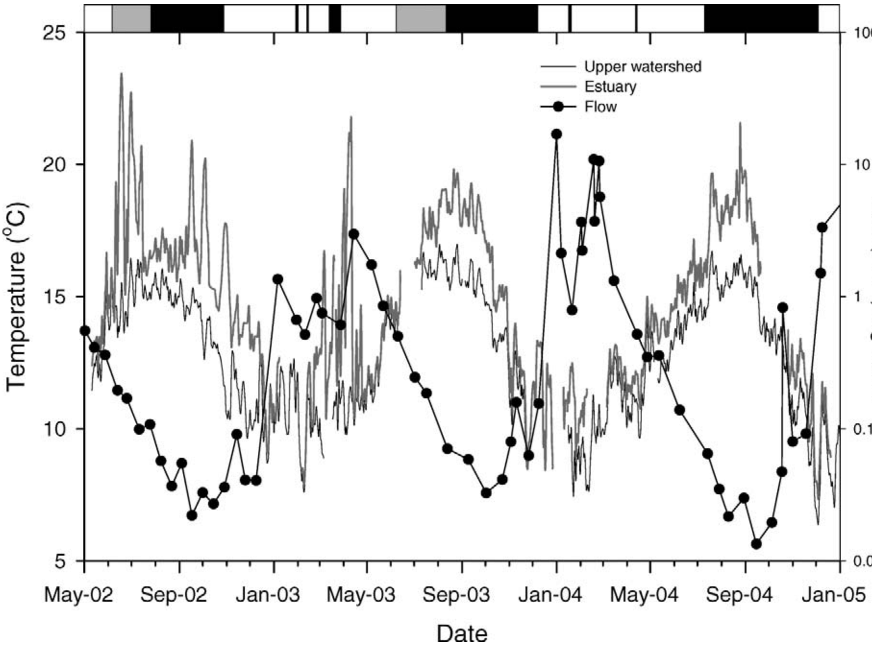


FIGURE 2.—Mean daily water temperature at upper and estuarine sites in the Scott Creek watershed, California (primary *y*-axis), and biweekly flow in the lower main stem (secondary *y*-axis) from May 2002 to January 2005. Shading in top bar represents estuarine status (white = open; gray = partially closed by sandbar; black = closed).

population, but this was assumed to be consistent across years.

Growth rate data were used to construct growth trajectories for various juvenile life history pathways. Initial age-0 growth rates were drawn from FL regressions developed from the results of upper-watershed growth. Confidence intervals (90% CIs) of the regressions were used to represent upper and lower growth curves. On this growth trajectory, age-0 fish were large enough to be PIT-tagged by the end of year 1. The SGR data from PIT tag recaptures were used to represent upstream growth (after December 31 of year 1) and estuarine growth. To obtain a daily estimate of growth, all intervals between successive recapture events greater than 7 d and less than 120 d from a given habitat were pooled, regardless of the number of recaptures per individual. Each interval spanning a particular day was interpreted as a growth rate observation on that day. Each day was spanned by a variable number of growth rate intervals (upstream mean = 15.7 d; estuarine mean = 34.1 d). We used a nonparametric smoother (Friedman 1984) to infer the central tendency of growth rate as a function of time. A 90% CI around this growth rate function was obtained by bootstrapping. Each bootstrap replicate was obtained by sampling with replacement from the pool of observed recapture intervals; the bootstrap intervals were converted as above to daily observations and a new growth-rate curve was estimated with the Friedman smoother for each bootstrap replicate. Two-hundred bootstrap replicates were made. For each day, the lower (upper) endpoint of the 90% CI for growth rate was the smoothed value for the 10th smallest (largest) of the 200 bootstrap-estimated growth rates. Bootstrapping and smoothing were done using the software package R (Ihaka and Gentleman 1996). Growth trajectories were completed by adding each day's growth to the sum of all previous days' growth. To portray these trajectories graphically, a base trajectory representing 4 years of growth in the upper watershed was plotted, and estuarine growth trajectories diverging from the upper-watershed line each summer were used to represent growth potentials of fish that migrated to the estuary.

Results

Environmental Data

Streamflow along the main stem varied by more than three orders of magnitude, from 0.013 m^3/s to over 17 m^3/s (Figure 2). Daily mean temperatures for the study period ranged from 5.6°C to 19°C in the upper watershed, and the overall mean was 10.3 ± 1.4°C. Daily mean temperatures in the estuary ranged from 7.4°C to 23.5°C and averaged 15.3 ± 3.1°C (Figure 2).

TABLE 2.—Growth rate estimates (±SE) for age-0 steelhead in Scott Creek, California, and multiple comparison test results for differences among years.

Year	Intercept Jan 1 (mm)	Growth rate (mm/d)[a]	R^2	n	Mean FL (mm)[b]	Date range
2002	20.73 ± 1.39	0.112 ± 0.006	0.203	1,370	46.12 ± 0.31	Jun–Nov 2002
2003	16.51 ± 1.63	0.139 ± 0.007	0.303	795	46.38 ± 0.45	Jun–Nov 2003
2004	22.32 ± 2.16	0.129 ± 0.010	0.280	471	50.72 ± 0.61	Jun–Nov 2004
Combined years	20.54 ± 0.72	0.119 ± 0.003	0.313	3,024	46.23 ± 0.23	Mar–Dec

[a] Multiple comparison tests: 2002 vs. 2003, $P = 0.004$; 2002 vs. 2004; $P = 0.101$; 2003 vs. 2004, $P = 0.417$.

[b] Multiple comparison tests: 2002 vs. 2003, $P = 0.878$; 2002 vs. 2004, $P = 0.001$; 2003 vs. 2004, $P = 0.001$.

During this study, a warm, relatively deep lagoon typically formed during summer (partially closed and closed; see Figure 2) when a sandbar formed at the mouth of the stream. However, the timing of formation varied from year to year. Except for occasional large wave events that pushed salt water over the sandbar and created haline stratification in deeper basins, the lagoon was primarily freshwater during summer and fall months.

Upstream Growth: Age-0 Fish

Newly emerged fry were observed between March and June of each year. We compared differences in growth rates for age-0 steelhead sampled at the upstream survey sites during June through November 2002–2004 (data were not consistently collected for all 3 years before June or after November; Table 2; Figure 3). Growth rates were approximately linear during the first 10 months of growth. Growth rates differed among the 3 years (heterogeneity of slopes test: $F = 4.288$, $P = 0.014$). A comparison of mean FLs revealed significant differences among years ($F = 26.309$, $P < 0.001$) as did comparisons using the Tukey post hoc analysis (Table 2). Mean growth rate per year was potentially influenced by several variables, including flow, temperature, age-0 coho salmon density, and age-0 steelhead density for each year (Table 3). Because only 3 years of data were available, no correlation analyses were performed and only raw data are presented.

We compared growth rates between untagged and elastomer-tagged individuals present at the same sites during June through November 2003. No significant

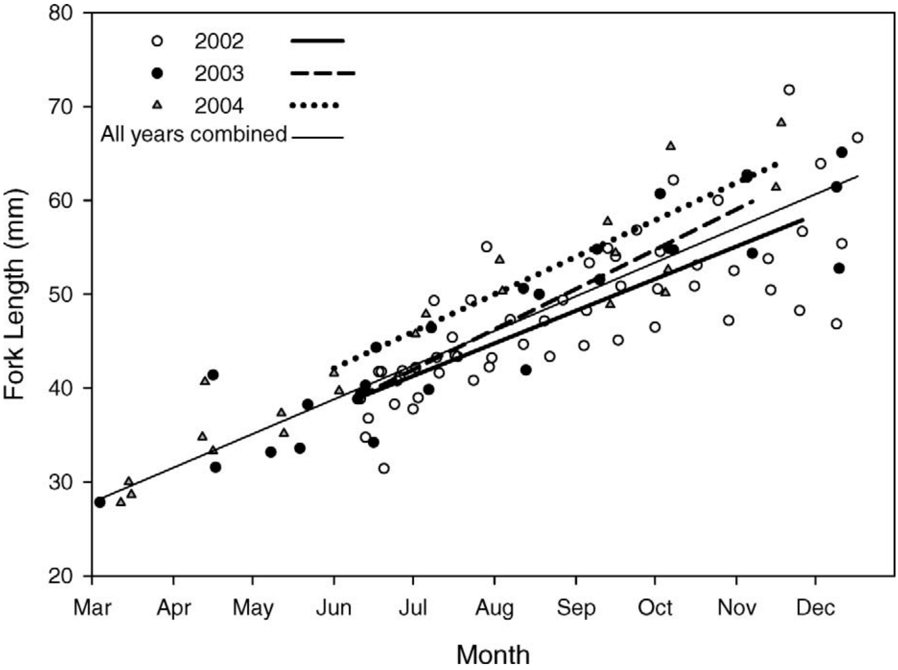


FIGURE 3.—Age-0 steelhead fork length (FL) over time in the upper Scott Creek watershed, California, 2002–2004. Symbols represent mean FL ($n \approx 20$ fish) at each of five age-0 sample sites. Linear regressions were calculated from raw data (not means) and are described in Table 2.

TABLE 3.—Age-0 steelhead growth rates relative to means of several biotic and abiotic variables measured in Scott Creek, California. Fish density is given as number of age-0 fish per 30.5 m.

Year	Growth rate (mm/d)	FL (mm)	Mass (g)	Water temperature (°C) (Jun–Nov)	Flow (m^3/s)	Coho salmon density	Steelhead density
2002	0.112	46.2	1.34	13.80	0.074	79.2	35
2003	0.139	46.4	1.63	14.44	0.132	1.5	55
2004	0.129	50.8	1.79	13.70	0.089	8.6	37

differences in growth rate between tagged and untagged fish were detected (heterogeneity of slopes test: $F = 0.953$, $P = 0.329$). The elastomer tagging of fish in June 2003 confirmed that many individuals remained at their original tagging sites and that growth measurements were at least partially based upon repeated captures of the same individuals.

Upstream Growth: Age-1 and Older Fish

We deployed 611 PIT tags in the upper watershed. We recaptured 114 fish at least once and several individuals were recaptured multiple times, yielding a total of 196 recaptures in the upper watershed between May 2003 and November 2004. The mean time interval between recapture events used in seasonal analysis was 55.3 ± 2.7 d ($n = 106$). At initial capture, mean FL was 104.3 ± 2.8 mm ($n = 106$) and mean mass was 15.6 ± 1.2 g ($n = 103$). With the onset of winter rains, mean individual growth rates increased, peaking at around 0.160% per day in April and then declining to less than 0.014% per day by August. Growth remained slow in the upper watershed until November. To compare growth rates for different times of year, data were binned into seasonal categories (fall = August–October; winter = November–January; spring = February–April; summer = May–July). Growth rates differed significantly among seasons for FL ($F = 12.5$, df = 4, $n = 106$, $P < 0.001$) and mass ($F = 8.4$, df = 4, $n = 99$, $P < 0.001$; Figure 4). Significance values for Tukey post hoc analysis of seasonal SGR differences in FL and mass are presented in Table 4.

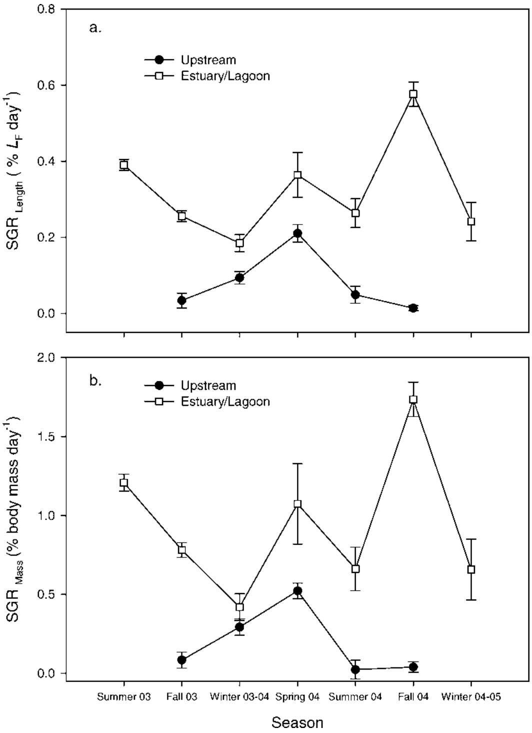


FIGURE 4.—Mean (±SE) specific growth rates (SGRs) of PIT-tagged steelhead recaptured in upper and estuary–lagoon habitats of the Scott Creek watershed, California, 2003–2005: **(a)** SGR_{FL} and **(b)** SGR_{mass}.

Estuarine Growth

We deployed 1,498 PIT tags in fish caught while seining the estuary or in the smolt trap at the head of the estuary between February 2003 and December 2004. Of these, 378 fish were recaptured at least once and some individuals were recaptured up to five times over the course of a year, resulting in a total of 994 recaptures in the estuary between May 2003 and December 2004 (mean recapture interval = 41.7 ± 1.6 d, $n = 311$). Mean FL at initial capture was 126.23 ± 2.0 mm ($n = 311$). Mean mass at initial capture was 28.4 ± 1.6 g ($n = 306$). To compare growth rates for different times of year, data were binned into the same seasonal categories defined above. Specific growth rates differed significantly among seasons for both FL ($F = 27.1$, df = 6, $n = 311$, $P < 0.001$: Figure 4) and mass ($F = 23.2$, df = 6, $n = 311$, $P < 0.001$). Results of Tukey post hoc analysis of seasonal SGR differences in FL and mass are presented in Table 5.

Mean SGRs (FL) in the estuary for summer and fall 2003 ($n = 147$), 2004 ($n = 104$), 2005 ($n = 87$), and 2006 ($n = 47$) were calculated and plotted against the number of fish in the estuary after the time of closure (Figure 5). This was accomplished by the PIT tagging of additional fish ($n = 1,205$) between January and November of 2005 and 2006. The difference in

TABLE 4.—Results of Tukey post hoc analysis testing for significant differences in juvenile steelhead growth between seasons in upstream habitat within Scott Creek, California. Bold type indicates P-values less than 0.05.

Season and year	Winter 2003–2004	Spring 2004	Summer 2004	Fall 2004
		FL (mm)		
Fall 2003	0.178	**<0.001**	0.955	0.823
Winter 2003–2004		**0.012**	0.502	**0.018**
Spring 2004			**<0.001**	**<0.001**
Summer 2004				0.399
		Mass (g)		
Fall 2003	0.115	**0.001**	0.905	0.944
Winter 2003–2004		0.295	**0.022**	**0.017**
Spring 2004			**<0.001**	**<0.001**
Summer 2004				0.999

estuarine growth rate among years is at least partially explained by differences in steelhead population size among years; there was a negative relationship between estuarine population size and growth ($R^2 = 0.9895$, $P = 0.005$), as described by the equation:

$$\mathrm{SGR_{FL}} = -0.0002(\text{population size}) + 0.8389. \tag{1}$$

Mean FL of smolts in the lagoon during the last fall sampling event was compared for 2003–2006 to determine whether length at the end of the summer–fall growing season varied between years. A significant difference was observed ($F = 29.3$, df $= 3$, $n = 526$, $P < 0.001$). However, Tukey post hoc analysis revealed that this effect was driven by 2003, which was the only year that differed; fish were significantly longer during that year than in the other 3 years ($P < 0.001$ for each comparison with 2003; Figure 5).

Comparisons of Estuarine versus Upstream Growth

Fish grew much faster in the estuary than upstream (Table 6; Figure 4). Coho salmon were typically absent from the estuary and were present in very low densities during the time upstream steelhead growth measurements were made with PIT tag recaptures. Summer temperatures in the upstream habitat were 14–18°C, while estuary–lagoon temperatures were warmer (from 15°C to ≥24°C).

Condition factor (mass/[length^3]) varied primarily as a function of season ($F = 14.26$, df $= 6$, $n = 1{,}204$, $P < 0.001$) and did not vary significantly between the two habitats ($F = 0.001$, df $= 1$, $n = 1{,}204$, $P = 0.971$). In general, the lowest condition factors in both habitats were observed in the spring and were presumably associated with smoltification (Hoar 1976).

Timing of Life History Decisions and Growth Trajectories

Most of the fish in this watershed migrate during the spring after their first or second winter, as shown in Figure 6, which provides the size frequency distribution of downstream migrants during spring 2004. Based on scale analysis ($n = 185$), fish under 120 mm FL were less than 2 years old. Once fish have begun the downstream migration, the tendency to

TABLE 5.—Results of Tukey post hoc analysis testing for significant differences in juvenile steelhead growth between seasons in the Scott Creek estuary, California. Bold type indicates P-values less than 0.05.

	Fall 2003	Winter 2003–2004	Spring 2004	Summer 2004	Fall 2004	Winter 2004–2005
			FL (mm)			
Summer 2003	**<0.001**	**<0.001**	0.999	**0.012**	**<0.001**	**0.039**
Fall 2003		0.583	0.557	1.000	**<0.001**	1.000
Winter 2003–2004			0.081	0.598	**<0.001**	0.949
Spring 2004				0.703	**0.007**	0.609
Summer 2004					**<0.001**	1.000
Fall 2004						**<0.001**
			Mass (g)			
Summer 2003	**0.002**	**<0.001**	0.995	**0.001**	**<0.001**	**0.024**
Fall 2003		0.137	0.818	0.981	**<0.001**	0.993
Winter 2003–2004			0.059	0.743	**<0.001**	0.885
Spring 2004				0.538	**0.028**	0.645
Summer 2004					**<0.001**	1.000
Fall 2004						**<0.001**

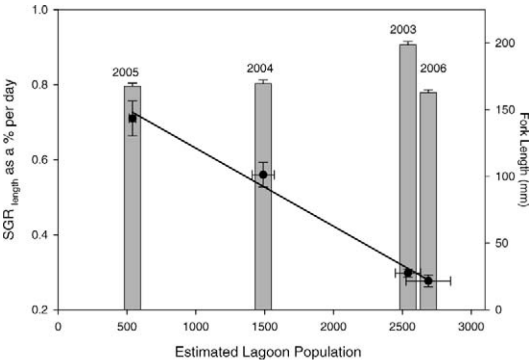


FIGURE 5.—Estimated annual lagoon population sizes and mean growth rates from 2003 to 2006 (left *y*-axis) The bar graph (right *y*-axis) represents mean fork length of fish sampled in the estuary in late fall of each year just before winter storm season and lagoon opening. Years match points within labeled columns. All data are means ± SE, $R^2 = 0.99$; regression $P = 0.005$.

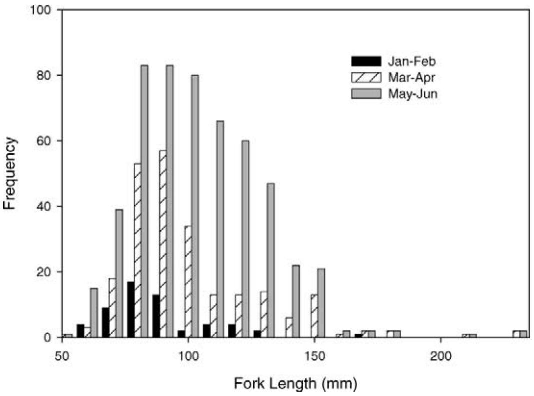


FIGURE 6.—Fork length frequency distribution (10-mm bins) for downstream-migrating steelhead in Scott Creek, California, during spring 2004. Data are grouped by 2-month intervals.

remain in the estuary or go to sea appears to be influenced by the timing of lagoon formation, which typically occurs sometime between May and August (Figure 2). In years when the lagoon forms later, juvenile steelhead densities are much lower, as many of the age-1+ downstream migrants appear to have left the watershed. Recruitment of age-0 steelhead to the estuary after the smolt run ends presumably occurs in response to reduced competition and predation from older fish in the lagoon or may simply be due to higher flows in wetter years, which contribute to delayed lagoon formation. These differences in density and age of recruitment to the estuary were observed during this study. The lagoon formed early (June) and recruitment was high (~2,540 fish) in 2003, whereas the lagoon formed later (July) and recruitment was much lower (~1,489 fish) in 2004. In addition, estuarine fish were significantly older ($t = 2.23$, $P < 0.002$, $n = 28$) and larger ($t = 2.04$, $P < 0.001$, $n = 124$) at the time of recruitment in 2003 (mean age = 1.52 years; mean FL = 152 mm) than in 2004 (mean age = 0.57 years; mean FL = 93 mm), confirming the large proportion of age-0 fish in 2004. This trend continued into 2005 (Figure 5), when the lagoon formed even later (August 26) and recruitment was limited to about 540 fish. In 2006, lagoon formation began in early June and followed a pattern similar to that in 2003. It is unlikely that recruitment to the lagoon was strongly influenced by total number of smolts. Although good estimates of smolt abundance among years were not available due to varying trap efficiency, the age-0 steelhead densities from the electrofishing surveys in the previous fall (Table 3) showed no relationship with lagoon population size observed during the subsequent summer.

TABLE 6.—Results of two-way ANOVA of the effect of habitat type (estuary and upstream) and season (fall 2003, winter 2003–2004, and spring–fall 2004) on juvenile steelhead specific growth rates (SGR) in Scott Creek, California (SS = sum of squares; MS = mean squares).

Factor	df	SS	MS	*F*	*P*
		SGRFL			
Habitat	1	3.031	3.031	106.336	<0.001
Season	4	1.465	0.366	12.848	<0.001
Habitat × season	4	2.382	0.595	20.892	<0.001
Error	303	8.637	0.029		
		SGRmass			
Habitat	1	24.392	24.392	72.095	<0.001
Season	4	16.368	4.092	12.095	<0.001
Habitat × season	4	22.587	5.647	16.691	<0.001
Error	296	100.144	0.338		

In this watershed, juvenile steelhead exhibit three life history pathways before ocean entry. The first pathway is direct recruitment to the estuary after spending only a few months in the upper watershed (Figure 7, pathway A). The second pathway is to spend 1–2 years rearing in the upper watershed, migrate downstream to the estuary, and remain there for an additional 1–10 months before ocean entry (Figure 7, pathway B). The third is to spend one or more years rearing in the upper watershed, migrate downstream, and enter the ocean (Figure 7, pathway C). Alternatively, fish exhibiting pathway C might never migrate and instead will carry out their life cycle in freshwater as residents. Based upon the growth rate data from this study, it is possible to model fish demonstrating different life history pathways and compare those with observations of the population at a given time. After

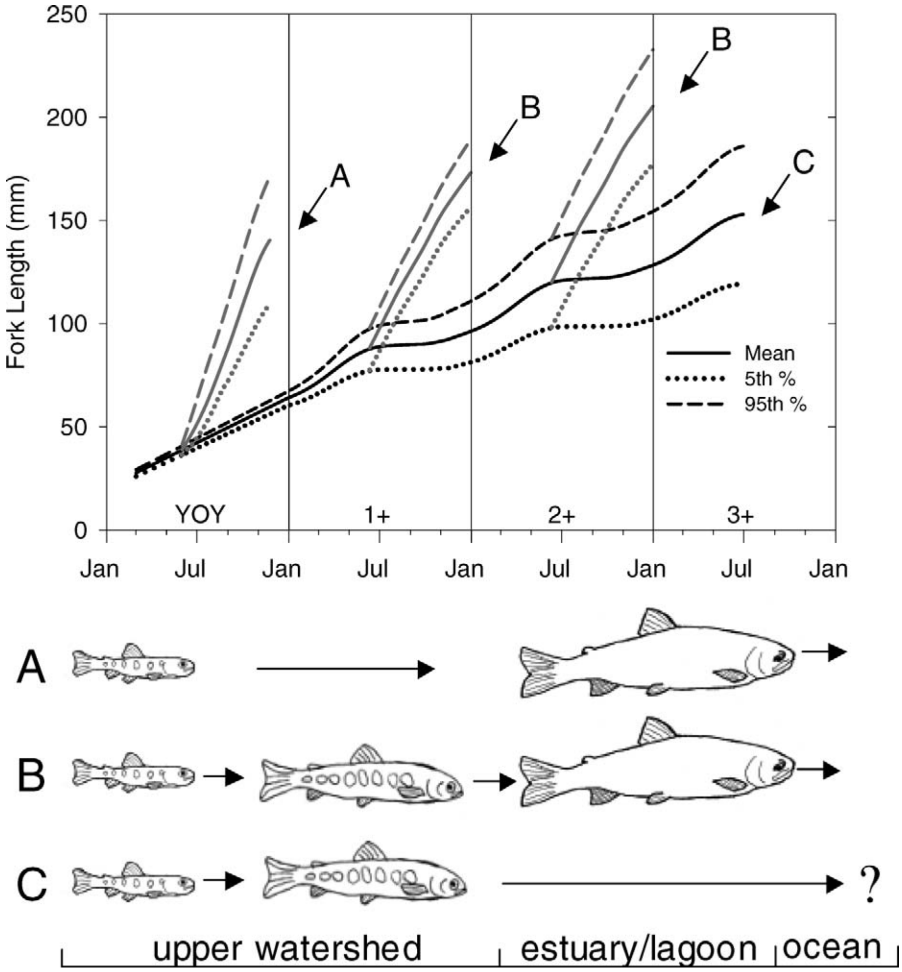


FIGURE 7.—Upper panel: growth trajectories of juvenile steelhead in the Scott Creek watershed, California, showing observed changes in FL determined from resampling of age-0 fish during the first 8–10 months and larger PIT-tagged individuals (ages 1–3 and older) that were recaptured in the upper watershed (black lines) or estuary (gray lines). All PIT tag recaptures were pooled within each habitat and were bootstrap sampled to determine central tendencies. Lower panel: the three freshwater life history pathways corresponding to A–C in the upper panel are illustrated (from left to right, size-classes are fry–age-0, parr, and estuary–lagoon residents). The question mark at the end of pathway C indicates the possibility that fish remain as residents in the creek.

hatching in the spring (Table 2), steelhead fry could migrate to the estuary during the summer (pathway A) and switch to an estuarine growth trajectory based on low densities (using data from summer 2004) or they could remain in the upper watershed, where growth is slower (see Table 2), and would reach 65 mm by the end of their first year. As fish entered their first winter, our measurements of growth transitioned from population means to measurements of known individuals (identified by PIT tags). Data collected from fish that were PIT-tagged in the upper watershed can approximate the size of fish during the subsequent May (the peak of the spring downstream migration). At this point, fish either spend another year in the upper watershed or begin their spring downstream migration. The predicted size range after 1–2 years of upstream growth (Figure 7) corresponds well with the observed downstream migrant sizes at ages 1 and 2 in this population (mean FL = 96.8 ± 1.1 mm, n = 641; Figure 6). After downstream migration, fish remaining in the estuary would probably follow a growth trajectory similar to that observed in the summer of 2003, when the lagoon began forming in June. While timing of lagoon formation tends to influence recruitment and growth rate, as the two are inversely related, the end result is that fish are of similar size by late fall

(Figure 5). Some larger downstream migrants may also depart the estuary before lagoon formation with only 1–2 months of additional growth.

Discussion

In this study, we reported growth rates of wild, free-ranging juvenile steelhead from the time of emergence to ocean entry in both upstream and estuarine habitats in a small stream along the central California coast. Growth rates were heavily influenced by local habitat and seasonal climate patterns. Specifically, growth in the upper watershed was limited and somewhat out of seasonal phase (mild winter, dry summer) with what would be expected from populations at higher latitudes or elevations, where fish exhibit slow growth during harsh winter periods (Chapman and Bjornn 1969; Wurtsbaugh and Davis 1977b). Estuarine growth, which has not been reported for steelhead previously, was much higher overall than growth in the upper watershed. Finally, growth patterns and movement suggest that steelhead pursue one of three life history pathways while rearing in various combinations of upper watershed and estuarine habitats. From the data collected, we were able to construct a growth model showing size at age for each freshwater life history pathway observed.

Growth of age-0 fish was measured over 3 years and varied significantly. While 3 years was insufficient to compare mean annual trends, several potential influences were apparent. For instance, age-0 steelhead growth was negatively associated with juvenile coho salmon density, which varied dramatically among years in this watershed due to the near extirpation of two year-classes (Hayes et al. 2004). This result was not surprising (Fraser 1969; Hearn 1987), and the reverse effect (i.e., steelhead density affecting coho salmon growth) has also been observed in other populations (Harvey and Nakamoto 1996). In addition, age-0 growth was positively associated with mean annual flow and mean summer–fall temperature in the upper watershed.

Growth of age-1+ fish in the upper watershed was slowest during the summer and fall, and in some cases individual fish actually decreased in FL. Age-0 steelhead densities were typically an order of magnitude higher than those of all older age-classes combined (J.J.S., unpublished data). Also, the majority of surviving fish migrated downstream after their first winter (Figure 6). In combination, these results indicate that the upstream watersheds are not very productive, presumably because of the low-flow environment and a low nutrient input under redwood canopies (Romero et al. 2005). This pattern of accelerated growth in the winter and spring (0.3–0.6% per day) and limited growth in the summer (0–0.2% per day) has been reported for foothill streams of the Sierra Nevada Mountains (Railsback and Rose 1999; Merz 2002) and other coastal California streams (Harvey et al. 2005), where growth rates were only 10–20% of potential maxima of 2.5–3.0% per day (Wurtsbaugh and Davis 1977b; Myrick and Cech 2005). These patterns are confounded by the fact that growth was slowest when temperatures were near the thermal optimum. While not quantified in this study, low summer flows in the upper tributaries may contribute to reduced wetted surface area for aquatic invertebrate production and terrestrial invertebrate drift, resulting in less food during a time when warmer temperatures are increasing metabolic rates of fish. Limited growth data exist across the latitudinal range of *Oncorhynchus* spp.; however, similar growth patterns were observed for coho salmon in coastal streams in Oregon and Washington (Breuser 1961; Bilby et al. 1996).

In comparison with upstream growth, growth rates in the estuary were much higher, which is probably due in part to the warmer summer and fall temperatures and differences in food availability as was reported for Atlantic salmon (Cunjak 1992). In Scott Creek, coho salmon did not use the estuary, presumably due to thermal preferences or tolerances (Stein et al. 1972); however, temperatures were at the thermal optimum for steelhead (17–19°C; Wurtsbaugh and Davis 1977b; Myrick and Cech 2005). Competition with coho salmon was probably not a major influence on differences in age-1+ steelhead growth between upstream and estuarine habitats, since the steelhead were larger than coho salmon fry and growth upstream was measured during a period of low coho salmon density. The estuary seemed to be a very productive habitat, particularly when in a lagoon state. Seining efforts were often difficult due to the large volumes of freshwater algae growing there and marine algae that were deposited by waves. Large numbers of invertebrates (amphipods *Eogammarus* spp. and *Corophium* spp.; shrimp *Neomysis* spp.; and isopods *Gnorimosphaeroma* spp.) were regularly observed in association with the algae. While comprising less than 5% of the total stream area, the estuary may be the most important habitat for steelhead growth in this watershed.

Estuarine growth rates were among the fastest reported for wild steelhead in the literature (1–2% per day), but did not reach the maximum (2.5–3.0% per day) observed in captivity for this species (Wurtsbaugh and Davis 1977b; Myrick and Cech 2005). Growth rates in the estuary varied among years and appeared to be density dependent: fish grew much faster in the estuary during years when recruitment was lower.

Recruitment was related to the timing of lagoon formation, when water began backing up behind a sandbar on the beach, forming a warm deep environment. Among years, the timing of sandbar formation varied by several months. The earlier the lagoon formed, the greater the population size. Although the growth rate was lower in these years, the longer growing season appeared to compensate for this, and fish were the same size or larger by the end of the season (Figure 5). In addition, short-term recruitment periods on the order of weeks to a couple of months have been observed in Scott Creek and other coastal California watersheds, wherein steelhead take advantage of a brief growth period and enter the ocean before sandbar formation (Smith 1990; Bond 2006).

A secondary issue explaining differences in estuarine growth rates among years relates to the age of fish recruiting to the estuary. In years when the lagoon formed late, age-0 fish recruited to the lagoon in higher proportions than in years when it formed early. In the laboratory, small fish grow faster than large fish under similar ration levels (Wurtsbaugh and Davis 1977a; Connolly and Peterson 2003). The age-0 steelhead that reared in the estuary entered the ocean 6–10 months after recruitment at a greater size with potentially greater chances of marine survival than the age-1+ fish that left before lagoon formation.

The high-resolution growth data collected over the entire juvenile life history cycle in this study enabled the construction of growth trajectories for this population. While not discussed here, it should be acknowledged that the decision to follow a particular pathway is probably due in large part to individual fish behavior and this system is more complex that fish simply growing in response to basic habitat conditions. The scope of this paper was to describe the common trajectories observed in this system. Independent confirmation of these trajectories was provided by data collected on the size and age of downstream migrants in the population (Figure 6), which were not used in creating the trajectories but match the predictions in Figure 7. These trajectories led to several different life history pathways. While such data have been collected for Atlantic salmon (Arnekleiv et al. 2006) and brown trout (Ombredane et al. 1998), comparable data sets are not common for Pacific salmon, presumably due to harsh winters that make the logistics of monitoring growth on a year-round basis more challenging.

In general, it appears that juvenile steelhead from this population migrate downstream before age 2,as very few fish greater than 150 mm or older than age 2 are observed among smolts. While the fish are still relatively small in size, their strategy is to take advantage of lagoon growth opportunities; overall, these fish probably enter the ocean within 6–10 months, and a majority enter the ocean before age 3. Detailed estimates of the relative proportion of fish following each strategy were beyond the scope of this study. In general, the distribution of size and age for downstream migrants was consistent between years (Bond 2006) and the age of fish recruiting to the estuary–lagoon was probably influenced by the timing of lagoon formation and varied between years. Withler (1966) and Busby et al. (1996) reviewed steelhead smolt age along the West Coast of North America and indicated that there is a general cline in freshwater residence time; steelhead from Alaska and British Columbia stay in freshwater for 3 years, whereas fish from Washington, Oregon, and California typically remain for 2 years and the frequency of 1-year-old smolts increases in southern parts of the range. It is unknown whether fish in southern populations are truly younger at ocean entry than those from northern populations. Fish in Scott Creek migrate downstream or undergo parr–smolt transformation at a younger age but then often spend additional time rearing in the estuary before ocean entry, an observation possibly missed by previous studies due to location of smolt traps upstream of the estuary (Shapovalov and Taft 1954), a lack of additional annulus formation, or both, as emigrating smolts transition from peak upper-watershed growth rates to even faster estuarine growth rates.

Marine survival measured in the Scott Creek watershed and across the steelhead range appears to be influenced by size at ocean entry, and generally fish smaller than 150 mm are unlikely to survive (Ward et al. 1989; Bond 2006). The southern coastal estuaries that form lagoons provide the opportunity for fish to achieve the necessary size for marine survival, which heavily influences adult escapement and possibly defines adult production from the watershed. However, it is not known how coastal California steelhead achieve sufficient size for marine survival in watersheds where upstream growth is limited and where estuaries dos not form summer lagoons, either due to natural geological and hydrological processes or anthropogenic processes (e.g., water consumption, stream mouth modifications, artificial breaching of sandbars). Even if very few adults are produced from systems without lagoons, there may still be sufficient numbers available in most years to replenish the stream with juveniles. At Scott Creek, lagoons suitable for rearing have been absent in many years over the last two decades due to artificial sandbar breaching, water diversion, and drought. However, juvenile abundance upstream was fairly consistent from 1988 to 2007 (J.J.S., unpublished data), possibly buffered by the iteroparous nature of steelhead. Alternatively, it may be that without a reliable presence of lagoons from year to year, populations may not be able to maintain anadromy. We could expect to see a higher proportion of fish pursuing resident life history paths in southern populations from systems where estuaries are lacking or have been compromised by development. Finally, estuaries in many systems also provide important growth opportunities for out-migrating smolts and brackish areas for the fish to adjust to salt water (Healey 1982); this would improve the ocean survival of the relatively small smolts reared in some watersheds like Scott Creek.

The steelhead population in this study and most California coastal stocks are federally listed as threatened under the Endangered Species Act, and stocks situated farther south are listed as endangered. As flows in these watersheds are at constant risk of being reduced even more by human consumption demands, this has become a critical management issue that will probably only increase in importance over time. In addition to the challenges of low flows in the upper watershed, there is a need to maintain connectivity with the estuary. Fish may need to take refuge from the estuary by moving upstream during periods of extreme temperature or low oxygen levels. In addition, summer flows must be low enough for sandbars to build up (thus forming the lagoon) but high enough that the lagoon does not leach through the sand bar (thus leaving only a shallow or dry creek bed).

Presumably, with increasing flows and nutrient contributions from marine (salmon carcasses) and terrestrial sources, upper-watershed habitats will become more productive as one moves north, trading off the loss of coastal summer lagoons as flows become too high for sandbars to close off streams. In addition, winter temperatures become limiting in the north, while summer temperatures are near the growth optimum (Hartman 1965). Therefore, fish in high-altitude or high-latitude river systems will probably grow better in summer than in winter and will follow different growth trajectories from those reported here.

Acknowledgments

Funding for this study was provided by the National Marine Fisheries Service, the Central Coast Salmon Restoration Program, and the Fisheries Restoration Grant Program. Constructive reviews were provided by Steve Lindley and Dave Rundio, several anonymous reviewers, and the associate editor. Field assistance was provided by Corey Phillis, Megan Atchenson, Ryan Weidling, Joanne Wong, Devon Pearse, Jeff Harding, and Jeff Perez. Landowner access was provided by Big Creek Lumber Company and California Polytechnic State University's Swanton Pacific Ranch. Animal studies were carried out according to and approved by the University of California–Santa Cruz Animal Use Committee based on National Institutes of Health guidelines.

References

Arnekleiv, J. V., A. G. Finstad, and L. Ronning. 2006. Temporal and spatial variation in growth of juvenile Atlantic salmon. Journal of Fish Biology 68:1062–1076.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53:164–173.

Bond, M. H. 2006. The importance of estuarine rearing to central California steelhead (*Oncorhynchus mykiss*) growth and marine survival. Master's thesis. University of California, Santa Cruz.

Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. Report NMFS-NWFSC-68.

Breuser, R. N. 1961. Foods and growth of juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), and Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum) in certain Oregon streams. Master's thesis. Oregon State University, Corvallis.

Busacker, G. P., I. R. Adelman, and E. M. Goolish. 1990. Growth. Pages 363–387 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27.

Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32:667–680.

Cannata, S. 1998. Observations of steelhead trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*) and water quality of the Navarro River estuary/lagoon May 1996 to December 1997. Draft report prepared for the Humboldt State University Foundation, Arcata, California.

Chapman, D. W. 1962. Aggressive behaviour in juvenile coho salmon as a cause of emigration. Journal of the Fisheries Research Board of Canada 19:1047–1080.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams with special reference to food and feeding. Pages 153–176 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. Institute of Fisheries, University of British Columbia, Vancouver.

Connolly, P. J., and J. H. Peterson. 2003. Bigger is not always better for overwintering young-of-year steelhead. Transactions of the American Fisheries Society 132:262–274.

Cunjak, R. A. 1992. Comparative feeding, growth and movements of Atlantic salmon (*Salmo salar*) parr from riverine and estuarine environments. Ecology of Freshwater Fish 1:26–34.

Elliott, J. M. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. Journal of Animal Ecology 44:805–821.

Fransen, B. R., P. A. Bisson, B. R. Ward, and R. E. Bilby. 1993. Physical and biological constraints on summer rearing of juvenile coho salmon (*Oncorhynchus kisutch*) in small western Washington streams. Pages 271–288 *in* L. Berg and P. W. Delaney, editors. Coho salmon workshop. Canadian Department of Fisheries and Oceans, Nanaimo, British Columbia.

Fraser, F. J. 1969. Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream channels. Pages 253–256 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. Institute of Fisheries, University of British Columbia, Vancouver.

Friedman, J. H. 1984. A variable span scatterplot smoother. Laboratory for Computational Statistics, Stanford University, Technical Report 5, Stanford, California.

Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 22:1035–1081.

Harvey, B. C., and R. J. Nakamoto. 1996. Effects of steelhead density on growth of coho salmon in a small coastal California stream. Transactions of the American Fisheries Society 125:237–243.

Harvey, B. C., J. L. White, and R. J. Nakamoto. 2005. Habitat-specific biomass, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 62:650–658.

Hayes, S. A., M. H. Bond, C. V. Hanson, and R. B. MacFarlane. 2004. Interactions between endangered wild and hatchery salmonids: can the pitfalls of artificial propagation be avoided in small coastal streams? Journal of Fish Biology 65(Supplement A):101–121.

Healey, M. C. 1982. Juvenile Pacific salmon in estuaries: the life support system. Pages 315–341 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Hearn, W. E. 1987. Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review. Fisheries 12(5):24–31.

Hoar, W. S. 1976. Smolt transformation—evolution, behavior, and physiology. Journal of the Fisheries Research Board of Canada 33:1233–1252.

Ihaka, R., and R. Gentleman. 1996. R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics 5:299–314.

Jones, M. W., and J. A. Hutchings. 2001. The influence of male parr body size and mate competition on fertilization success and effective population size in Atlantic salmon. Heredity 86:675–684.

Jones, W., W. S. C. Gurney, D. C. Speirs, P. J. Bacon, and A. F. Youngson. 2002. Seasonal patterns of growth, expenditure and assimilation in juvenile Atlantic salmon. Journal of Animal Ecology 71:916–924.

Levings, C. D., C. D. McAllister, and B. D. Chang. 1986. Differential use of the Campbell River estuary, British Columbia (Canada), by wild and hatchery-reared juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 43:1386–1397.

Merz, J. E. 2002. Seasonal feeding habits, growth, and movement of steelhead trout in the lower Mokelumne River, California. California Fish and Game 88(3): 95–111.

Miller, B. A., and S. Sadro. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. Transactions of the American Fisheries Society 132:546–559.

Myrick, C. A., and J. J. Cech. 2005. Effects of temperature on the growth, food consumption, and thermal tolerance of age-0 Nimbus-strain steelhead. North American Journal of Aquaculture 67:324–330.

Narver, D. W. 1969. Age and size of steelhead trout in the Babine River, British Columbia. Journal of the Fisheries Research Board of Canada 26:2754–2760.

Narver, D. W., and B. C. Andersen. 1974. Fish populations of Carnation Creek and other Barkley Sound streams—1970–1973: data record and progress report. Fisheries Research Board of Canada Manuscript Report 1303:115.

NMFS (National Marine Fisheries Service). 2006. Endangered and threatened species: final listing determinations for 10 distinct population segments of West Coast steelhead. Federal Register 71:3(5 January 2006):834–862.

Ombredane, D., J. L. Bagliniere, and F. Marchand. 1998. The effects of passive integrated transponder tags on survival and growth of juvenile brown trout (*Salmo trutta* L.) and their use for studying movement in a small river. Hydrobiologia 372:99–106.

Parker, R. R., and P. A. Larkin. 1959. A concept of growth in fishes. Journal of the Fisheries Research Board of Canada 16:721–745.

Peterson, N. P., E. F. Prentice, and T. P. Quinn. 1994. Comparison of sequential coded wire and passive integrated transponder tags for assessing overwinter growth and survival of juvenile coho salmon. North American Journal of Fisheries Management 14:870–873.

Quinn, T. J. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.

Railsback, S. F., and K. A. Rose. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Transactions of the American Fisheries Society 128:241–256.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletins of the Fisheries Research Board of Canada 191:382.

Romero, N., R. E. Gresswell, and J. L. Li. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. Canadian Journal of Fisheries and Aquatic Sciences 62:1797–1807.

Schwarz, K. M., and A. R. Orme. 2005. Opening and closure of a seasonal river mouth: the Malibu estuary barrier lagoon system, California. Zeitschrift fuer Geomorphologie Supplementband 141:91–109.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*). California Department of Fish and Game, Fish Bulletin 98.

Smith, J. J. 1990. The effects of sandbar formation and inflows on aquatic habitat and fish utilization in Pescadero, San Gregorio, Waddell and Pomponio Creek estuary/lagoon systems, 1985–1989. Report prepared by San Jose State University under Interagency Agreement 84-04-324 for the California Department of Parks and Recreation, Sacramento, California.

Stein, R. A., P. E. Reimers, and J. D. Hall. 1972. Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall Chinook salmon (*O. tshawytscha*) in Sixes River, Oregon. Journal of the Fisheries Research Board of Canada 29:1737–1748.

Thorpe, J. E. 1977. Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. Journal of Fish Biology 11:175–184.

Tschaplinski, P. J. 1987. The use of estuaries as rearing habitats by juvenile coho salmon. *In* T. W. Chamberlin, editor. Pacific Biological Station. Proceedings of the workshop: applying 15 years of Carnation Creek results. Pacific Biological Station, Nanaimo, British Columbia.

Ward, B. R., P. A. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:1853–1858.

Withler, R. E. 1966. Variability in life history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific coast of North America. Journal of the Fisheries Research Board of Canada 23:365–393.

Wurtsbaugh, W. A., and G. E. Davis. 1977a. Effects of fish size and ration level on the growth and food conversion efficiency of rainbow trout, *Salmo gairdneri* Richardson. Journal of Fish Biology 11:99–104.

Wurtsbaugh, W. A., and G. E. Davis. 1977b. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. Journal of Fish Biology 11:87–98.