Jarrod Ludwig
11/07/2022
California Salmonine Paper
Independent Study

Insight into the Salmonines of California

California is home to an astounding 32 distinct species of salmonids with 20 of them being endemic and 21 of them being anadromous species, depicting the necessity of the Pacific Ocean. The California Current is one of the most productive regions in the world which many of these species utilize during their growth and maturation into reproductive adults (Moyle 2002). The cold California Current flows from North to South, down the California coastline bringing nutrient-rich productive water. With such a productive system, it has been colonized by many marine species such as Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*). These species are an important piece of California's history because they hold high cultural and economic importance and are umbrella species for the conservation of the greater aquatic environment as well as sentinel species as their presence helps sustain the biota associated with them (Moyle *et al.* 2017).

1. Chinook salmon

1.1. Life History

Chinook salmon is an anadromous species with different runs, each having similar life histories, but different timing of spawning migrations. There are four runs of Chinook (fall, late fall, winter, and spring) which are differentiated by genetic differences, maturity of adults entering freshwater, location of spawning, duration of incubation, and outmigration of juveniles to the ocean (Moyle 2002). Adult salmon will migrate from the feeding grounds in the Pacific Ocean to begin their ascent up their natal rivers in which they were born. When spawning is close to occurring, females will create redds or nests in the riverbed, in which they will deposit their eggs for males to fertilize. Here, the fertilized eggs will incubate until hatching occurs, which is directly related to water temperature, dissolved oxygen, and substrate permeability (Kondolf and Wolman 1993).

Chinook salmon use the largest gravel of any California salmonine (up to 10% of their body length) as water flows through large interstitial spaces removing metabolic wastes and increasing oxygen availability, which is critical for the health of developing embryos (Kondolf and Wolman 1993). Gravel size was found to be significantly correlated with Chinook alevin growth and survival with increasing porosity of gravel being beneficial for the alevin (Merz *et al.* 2004). Water temperatures must be between 5 and 13°C and have oxygen near saturation for optimal embryo survival, as water temperatures exceeding 16.7°C in Sacramento River have created 82% mortality in salmon (Moyle *et al.* 2017). Under these conditions, embryos hatch in 40-60 days and will remain in the gravel as alevins for four to six weeks until their yolk sacs are absorbed (Moyle *et al.* 2017). As the alevins grow into juveniles, they often occupy pools with protection from avian predators and will use these food-rich flows at night to feed. Historically, juveniles would use off-channel habitats such as wetlands or floodplains as they are nutrient-rich with plankton and macroinvertebrates, but because of the expansion of agriculture from the late 1800s through the mid-1900s, California's landscape has been eliminated of roughly 95% of the state's wetlands (Hanak *et al.* 2011). Juveniles will rear in these stream waters for about one-year post-hatch and in spring will begin smoltification (Chinook salmon species profile 2022). Smoltification induces changes for the juvenile consisting of hypo-osmoregulation ability, metabolic and endocrine adaptations, and behavioral changes. When smoltification is complete while migrating downstream, the young adults are ready for entering the ocean. The length of their ocean life depends on how old they were when entering the ocean and marine conditions, water temperature being a large factor. The first step is the rearing phase for young adults as they occupy coastal waters before heading out to deeper depths. The California Current brings abundant food, such as small shrimp through upwelling events, to the coastal waters. Sub-adults will begin to feed on Pacific anchovies, juvenile rockfish, and Pacific herring at depths of 20-40 meters before moving offshore because of lower water temperatures, increased prey availability, and reduced potential predation risks (Moyle *et al.* 2017).

1.2. Diet

Historical diets of salmon off the coast of California consisted of krill, juvenile rockfish, and anchovy (Merkel 1957). Other invertebrates besides krill appear to be dominant in the ecosystem. In a study by Lavaniegos and Ohman (2007) on zooplankton communities, copepods and krill consisted of 90% of the carbon biomass meanwhile pelagic tunicates such as salps and pyrosomes only were 3.4%. However, tunicates represented 5% of carbon biomass in Southern California, but 13% in Central California. April appears to be near the annual peak for copepods carbon biomass and copepods have shown to resemble short-term variability in the ocean and long-term patterns can indicate climate-driven changes in transportation of source waters throughout the ocean (Copepod Populations 2019). Generally, copepods transported from the south of California or far offshore contain a greater variety of species, but are less nutritious for prey fish of salmon. Copepods descending from the north have a lesser species richness than the south but are more nutritious. Richness of southern copepod species was the highest observed during the 22-year monitoring from 2015 to the summer of 2017, due to an unusually long period of warm water conditions (Copepod Populations 2019). Northern copepod species are important because they are high in fat content and help many fishes grow and survive over winter. With the dominance by southern copepods, prey fish of juvenile salmon may be consuming the nutrient poor copepods leading to decreases in juveniles surviving to adulthood (Copepod Populations 2019). For krill (euphausiids), variability should be expected at different times of the year and spatial variability is highest in Central California compared to Southern California (Lavaniegos and Ohman 2007). Highest krill biomass appeared to be in July and August. In areas of northern California and central Oregon, slowed upwelling in spring and summer of 2005 showed catastrophic reduction in two species of euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*). In contrast waters in southern California were relatively unaffected, demonstrating great spatial variability in the California Current (Lavaniegos and Ohman 2007). The lack of krill species caused colony abandonment and massive reproductive failure by auklet sea birds in 2005, all following an El Niño or warm water event. Other prey species which have been historically significant in the diet of salmonines are rockfish. Many species of rockfish have been decimated by fishing pressures and resulted in the closing of the U.S. West Coast continental shelf fishery in 2003 (Field *et al.* 2010). Fishing has reduced the adult rockfish population limiting recruitment, but also ocean conditions and limited upwelling events has caused declines in juvenile populations.

Recent diet analysis has indicated that the main prey items of Chinook salmon are northern anchovy, juvenile rockfish, euphausiid krill, Pacific sardine, crab megalopae (*Cancer spp.*), Pacific herring, and market squid (Thayer *et al.* 2014). However, there has been a decrease in the number of rockfish, krill, herring, and squid in the diet, meanwhile sardine and anchovy have increased in importance (Thayer *et al.* 2014). When sardine population is large, they are present from the tip of Baja California to southeastern Alaska and throughout the Gulf of California, with migrations as far north as British Columbia in summer and back to southern California and Baja California in the fall (Kuriyama *et al.* 2020). Sardine and anchovy populations have varied over a period of 60 years, but sardines are much more variable than anchovies (Kuriyama *et al.* 2020). Sardine declines have lasted an average of 36 years and recoveries another 30 years (Kuriyama *et al.* 2020). It had appeared sardines recovered in the 2010s, but their populations have been declining again recently (Hill *et al.* 2011, Kuriyama *et al.* 2020). Anchovies have recently been on the rise as a dominant prey species, much of the increase in abundance is due to warming ocean waters leading to the northward expansion of the anchovy's range (NOAA Fisheries 2022). Prey trawls for abundance measurements over the last five years have reflected this uptrend in population (Figure 1).

2. Coho salmon

2.1. Life History

Like Chinook, coho salmon are an anadromous species and semelparous. Coho salmon life history is like that of Chinook salmon where adults spawn in streams and eggs will incubate in the substrate during winter and hatch in spring. Coho salmon were studied to determine relationships between their fecundity and egg sizes, and it was found fecundity and egg size are inversely related and northernmost populations produce more but smaller eggs (Flemming and Gross 1990). This variation could be because of trade-offs as large eggs produce larger juveniles to be competitively superior and less vulnerable to predators (Fowler 1972). However, large eggs don't survive well in poor gravel quality making habitat and spawning ground quality an important factor for egg incubation (van den Berghe and Gross 1989). The juveniles will hold in the stream for about a year before smoltification occurs and will travel downstream and out to the ocean (Groot and Margolis 1991). Coho salmon spend about 18 months out in the ocean before making their trip back to their natal stream, with optimal water temperatures in the range of 7.2-15.6°C.

In California, it has been suggested coho salmon remain 150 km off the shoreline (continental shelf) for a few months before dispersing (Shapovalov and Taft 1954). Feeding grounds are believed to have been over the continental shelf at depths of less than 90 meters (Milne 1950). When entering the sea, smolts move northward along the coast and some will reach the coastal waters of central Alaska by late summer (Groot and Margolis 1991). After about 12 months in the ocean, coho salmon will begin their migration back to their natal stream along the coast in depths up to 30 m. The diet of adult coho salmon is very similar to that of Chinook salmon, but it consists of about one-fifth of invertebrates meanwhile it is less than 3% in Chinook (FRBC 1955). Historical diets of coho salmon off the coast of Washington and Oregon included sardines and rockfish, with anchovies and smelts being insignificant (Silliman 1941). Ultimately, smolt to adult survival has been associated with variability in water temperature and productivity levels of the ocean. Cool waters and productivity have brought high survival rates for hatchery-raised coho, and the opposite has resulted in poor returns (Peterson *et al.* 2010). The presence of Chinook and coho salmon in ocean waters increases with the increase of chlorophyll concentrations and an increase in depth along with decreases in water temperature (Bi *et al.* 2007). In warm water years, the ocean habitat and feeding grounds for coho salmon become more fragmented where it generally is the entire coastal shelf. It was noted that yearling Chinook and coho salmon habitat overlaps in inner shelf waters, but Chinook yearlings did not range as far out to sea as coho suggesting a near shore preference (Peterson *et al.* 2010). In June, yearling coho and Chinook salmon had their highest abundances off the coast of Washington and Vancouver Island. But by September, most yearling Chinook had left and coho salmon remained (Fisher *et al.* 2007). Using coded-wire tags, it was found yearling coho salmon are less migratory in their first summer at sea than yearling Chinook as they are abundant off the coast of Washington, whereas Chinook move north rapidly to the northern Gulf of Alaska waters by August (Pearcy and Fisher 1988).

3. Steelhead trout

3.1. Life History

In California, steelhead trout is an anadromous species and iteroparous, but has some resident fish. Generally, most fish will smolt and emigrate at either age 1 or age 2, but it has been an ever-increasing trend for some fish to become residents whether by a plasticity response to the environment or by genetic changes (Satterthwaite *et al.* 2010). Declines in marine survival from smolts to adults have models predicting a change in life history. The current anadromous life history in California's Central Valley (CCV) steelhead is threatened by water management through water diversions and interrupted releases as cold-water releases are often needed in summer and early fall. This is also troublesome as cold water in late fall is important for the start of adult Chinook salmon holding and spawning (Satterthwaite *et al.* 2010, U.S. Department of the Interior 2008). Interbreeding has been known to occur between rainbow trout and steelhead trout, producing progeny that can be anadromous or nonanadromous (Zimmerman and Reeves 2000). Residency trout reach sexual maturity typically around 2-3 years of age (Moyle 2002). Migratory steelhead trout spend 2-3 years in freshwater, up to 6 years at sea (usually 2), and then return to spawn (Willson 1997). Populations in Oregon and California consist of higher frequencies of fish maturing in the ocean after one year compared to northern populations

(Busby *et al.* 1996). Central and southern California steelhead have populations dominated by fish maturing at age 3 (2 smolt/1 ocean) compared to age 4 (2 smolt/2 ocean). Most California steelhead begin spawning in December; however, winter steelhead are ocean-maturing and summer steelhead are stream-maturing meaning they enter freshwater up to a year before spawning (Busby *et al.* 1996). Frequently, smolting will occur in California steelhead after two years in freshwater, but hatchery conditions can allow smolting to occur in one year. With steelhead trout being iteroparous, frequency of multiple spawning is variable within and among populations.

3.2. Diet

Greatest feeding appears to occur in winter of individuals sampled in the Mokelumne River (Merz 2002). Filamentous algae were observed in 43% of stomachs, 10% contained chinook salmon and steelhead trout eggs and juveniles, bird feathers in 8%, and small mammal hair in 1% of stomachs. Most of the diet of steelhead composes of immature stages of aquatic insects such as hydropsychid and Diptera larvae. Increased fish size and water temperature has resulted in higher metabolism rates and subsequently food demands by juvenile steelhead, leading to shifts in stream habitat to account for such changes (Smith and Li 1983). When steelhead smolts begin to migrate towards the ocean, they enter the northern California Current in late spring and spend very little time in coastal waters and go directly offshore from Washington and Oregon in May and are gone in June (Daly *et al.* 2014, Myers 2018). For early marine residence of steelhead, prey consumed mostly consisted of rockfish, krill, Cancer crab larvae, euphausiids, and clupeids such as northern anchovy, all of which varies interannually and between warm and cold ocean regimes (Thalmann *et al.* 2020).

4. Population Abundances

4.1. Conservation Status

Historically, there has been a decline in adult returns for Chinook and coho salmon and steelhead trout. Populations of Chinook salmon have reached 1-2 million spawners annually across all runs but have declined significantly to less than 300,000 spawners (Figure 2). In 2008 and 2017, returns were so low as the fishery was mandated to be closed those years (Yoshiyama *et al.* 1998). Data from NOAA, federal, local, and state agencies, and the California Department of Fish and Wildlife have classified each run and species based on their level of concern for conservation under the Endangered Species Act.

The status of many of the runs are listed at high and critical levels of concern (Table 1; Moyle *et al.* 2017). Chinook salmon fall and late fall-run in the Upper Klamath-Trinity Rivers are not listed but are listed as of concern in CCV (Statewide Status 2021). Since the 1990s, hatcheries have produced nearly half the population in the Trinity and CCV rivers. The Sacramento River Chinook salmon winter-run is listed as endangered. Livingston Stone National Fisher Hatchery supports the production of this run and has reintroduced them into Battle Creek and the McCloud River where they were extirpated. Lastly, the Chinook salmon Upper Klamath-Trinity River spring-run is not listed, but CCV spring-run is threatened. The Feather River hatchery produces a hatchery spring-run, meanwhile Battle, Butte, Mill, and Deer creeks maintain a wild stock.

For the coho salmon population in California, the Central California Coast are endangered and the southern Oregon/Northern California Coast are threatened (Figure 3). About 30% of Iron Gate Hatchery and Trinity River steelhead are hatchery fish. Steelhead trout populations have been significantly impacted with Northern California, Central California Coast, South-Central California Coast, and CCV all listed as threatened. The Klamath Mountains Province steelhead are not listed but southern California steelhead are endangered (Figure 4). The Trinity and Smith Rivers provide about 64% of the average returning adults of steelhead trout.

4.2. Reasons For Decline

With many of the populations listed as threatened or endangered, it is important to understand the factors causing such an impediment on their success.

4.2.1. Dams and Water Diversions

The first major factor for salmon populations declines was the construction of dams on many rivers which the salmon and trout would run for reproduction. For example, the endangered winter-run Chinook no longer have access to their historic spawning grounds in the Pit, McCloud, Fall and Little Sacramento rivers, because of the Keswick Dam. Dams have been seen to create many secondary effects further than being impassable. Fining of sediment size by dams has been studied as larger gravel erodes away but is not replaced by upstream material as the dams block this cycling, making spawning material improbable to find (Merz *et al.* 2004). Also, dams can create pools of cooler water in the summer, even though most of the cool water is upstream. If released strategically, it can benefit these salmon downstream, but lack of cooler water has been seen as an issue for spring-run Chinook salmon as they need cooler water from snow melt in March and April when they enter the streams for spawning and the winter-run are already in the streams from March up until early August (Moyle *et al.* 2017, Statewide Status 2021). These pools often become too warm in winter compared to upstream temperatures (Merz *et al.* 2004). The warming water has also been caused by water diversions for hydroelectric facilities which has caused the cooler water to be diverted away from spawning habitat for these runs (Thompson *et al.* 2012). Lack of flowing water and low turbidity flows has also shown to reduce the diversity of the benthic invertebrate community, a food supply juvenile salmon rely on (Moyle *et al.* 2017).

4.2.2. Water and Habitat Degradation

Runoff from the surrounding land entering streams has created significant pollution from urbanization and agriculture. Agriculture is a large contributor to water degradation as it has created the removal of instream habitat and erosion through the creation of levees and channelization but also through sedimentation into the river (Moyle *et al.* 2017). Irrigation has produced reduced water levels declining cold water reserves for the salmon. Logging has further declined the habitat of spawning salmon as they require riparian ecosystems for growth of embryos and juveniles but also reduced vegetation on land has led to increased sediment in the rivers, filling in spawning sites (Moyle *et al.* 2017).

4.2.3. Climate Change

It has been well documented the impacts of climate change will be the most significant factor to hinder salmonine populations. Increased temperatures will warm fresh and ocean water which is lethal to these species, reduce snowpack which decreases snowmelt flows in spring, create larger variations in precipitation and drought, increase ocean acidity which may damage reefs and the productive ecosystems supported by coral, change the dynamics of marine and freshwater food webs which ultimately reduces the distribution, abundance, and survival of salmonine species (Moyle *et al.* 2017).

4.2.4. Thiamine Deficiency Complex

The most recent cause for decline of California salmonine species has been through thiamine deficiency complex (TDC). TDC is the inability of the mother to retain or obtain thiamine to pass on to her progeny for their development which may result in poor appetite, muscle atrophy, convulsions, loss of equilibrium, edema, poor growth, and increased sensitivity to physical disturbance or light (Halver 1972, Morito *et al.* 1986). Ultimately, this can result in early mortality of embryos. TDC was first discovered in the hatchery fry of CCV in 2020 (Mantua *et al.* 2021). The ailment of the fry was determined as TDC because when treated with thiamine baths, fry recovered and the symptoms of TDC were reversed. Since the first signs of TDC, egg and fry thiamine baths as well as thiamine injections to pre-spawn females have been used as methods to mitigate early mortality due to TDC (Futia *et al.* 2017). The first indications of TDC launched a state-wide egg monitoring program to evaluate several populations of Chinook salmon, coho salmon, and steelhead trout who were also found to have TDC. Lethal concentrations of thiamine in the eggs resulting in 50% mortality (LC_{50}) for Chinook salmon was evaluated at 2.7 nmol/g and for close to 100% survival of embryos 80 to 120-day post-fertilization, egg thiamine concentrations need to be greater than 5 nmol/g (Lindley 2021). These data established the following egg threshold values for the monitoring program: < 5 nmol/g of thiamine as low, 5-8 nmol/g as intermediate, and > 8 nmol/g as high. Monitoring throughout 2020, 2021, and 2022 revealed continuing declines of thiamine concentrations in CCV Chinook populations with very little effects to Northern California populations in the Klamath River system (Figures 5 and 6).

There have been two proposed hypotheses for the cause of thiamine deficiency in fish. The first one is the high fat content in the prey fish which results in lipid peroxidation, as noted in the Baltic Sea with sprat (*Sprattus sprattus*) and in the Great Lakes with alewife (*Alosa pseudoharengus*) (Alvarez *et al.* 1998, Keinänen *et al.* 2012, Futia and Rinchard 2019). Prey fish high in fats contain increased concentrations of polyunsaturated fatty acids (PUFA), which increase the risk of peroxidation. A PUFA is peroxidized when it encounters a hydroxyl radical, which is frequently generated by cellular metabolic processes (Lehninger 1970). The hydroxyl radical extracts a hydrogen atom from the methylene group of the PUFA and leaves a carbon radical. The carbon radical will rearrange itself to form a conjugated diene which reacts easily with oxygen (O_2), which is a product of many enzymatic processes. When the conjugated diene reacts with the O_2, it forms a peroxyl radical which can extract a hydrogen atom from other PUFAs to form a lipid peroxide and another carbon radical, fulfilling the propagation step. The lipid peroxide eventually breaks down into a compound such as an alcohol, which can lead to cell death and damage to the tissue. For the body to stop the propagation step from occurring, thiamine is used as an antioxidant to trap the lipid peroxyl radical in an unreactive state by donating a hydrogen atom. This causes thiamine reserves to be depleted and prey no longer have a significant amount of thiamine to pass to their predators. Research in the Baltic Sea on Atlantic salmon (*Salmo salar*) has also shown depleted levels of carotenoids, particularly astaxanthin which acts as an antioxidant, in fish experiencing syndrome M74 (thiamine deficiency) (Pettersson and Lignell 1998). Astaxanthin is deposited in the eggs with mobilized pigment from flesh of salmonids into the ovarian tissues during sexual maturation (Torrisen *et al.* 1989, Watanabe and Miki 1993, Hatlen 1997). It potentially acts as a protectant against UV radiation or prooxidants as well as chain terminators of propagation as fish diets containing astaxanthin reduced plasma levels of lipid peroxidation products (Krinsky 1993, Chew 1995, 1996, Bell *et al.* 2000). Vitamin E (α-tocopherol) is also an antioxidant used by the body and was at low concentrations in fish experiencing syndrome M74 (Börjeson and Norrgren 1997). Astaxanthin and vitamin E are the primary lipid-soluble antioxidants and eliminate the propagation step as well as quench singlet oxygens (Gorman *et al.* 1984, Burton and Ingold 1989).

However, not only will thiamine be deficient through lipid peroxidation, but it can impact the concentrations of PUFAs in the salmonine. PUFAs are needed in the diet at specific ratios as they are critical in adult reproduction and embryo development and survival. PUFAs in the bodies of adults have shown to increase fecundity, fertilization, and egg quality (Frémont *et al.* 1984). Consumption of prey rich in dietary PUFAs must be several months before spawning in salmonine species as they can have up to a 6-month period of vitellogenesis to incorporate the PUFAs into the egg yolks (Frémont *et al.* 1984). One of these essential PUFAs is docosahexaenoic acid (DHA, 22:6n-3) as it has shown to increase the weight of larval fish and their ability to resist osmotic shock (Izquierdo *et al.* 2001). PUFAs generate metabolic energy (ATP) and allow normal cell and cell membrane function particularly during development in cold winter waters and provide precursors for growth and development of the embryo (Pickova 1998, Appert 2022). The ratio of PUFAs and total amount in general is especially important as a higher ratio of AA (arachidonic acid, 20:4n-6): EPA (eicosapentaenoic acid, 20:5n-3) has been linked to increased egg quality, disease resistance, and growth. Dietary n-3 and n-6 PUFAs are essential fatty acids (EFA) for vertebrates and requirements of n-3 fatty acids are satisfied in marine organisms by EPA and DHA. A ratio of 2:1 for DHA: EPA indicates healthy embryonic development, but a higher ratio has been linked to early mortality syndrome in brook trout (Appert 2022). The protein content of squid with their concentrations of PUFAs as well as the lipid fractions in raw krill were found to improve egg quality of gilthead seabream (Izquierdo *et al.* 2001). However, diets with lipids above 10-20% of dry weight diet can cause excessive deposition of lipids in tissues (Czesny *et al.* 2009, Sargent *et al.* 2002). Krill and calanoid copepods are abundant in wax esters and cause fish tissues and eggs to be rich in 20:1n-9 and

22:1n-11 (Sargent *et al.* 2002). Significantly higher ratios of EPA:DHA was found in sardine and anchovies.

The other hypothesis is the presence of an enzyme, called thiaminase, which degrades thiamine in the prey of the salmonines. Thiamine is very sensitive to heat and neutral or alkaline solutions, but also to thiaminase as it will be broken down into its pyrimidine and thiazole moieties (Halver 2002). Thiamine hydrochloride and thiamine mononitrate have been used as the active vitamin in diets to build the reserves of salmonines but have been shown to be broken down and unusable through thiaminase activity and increased temperature. Clupeids such as alewife, sardines, herring, and anchovies in several ecosystems such as the Baltic Sea, Laurentian Great Lakes, and in ocean waters off the coast of California, have induced thiamine deficiency as they are some of the largest producers of thiaminase by an aquatic organism (Greig and Gnaedinger 1971, Tillit *et al.* 2005, Honeyfield *et al.* 2005, Wistbacka and Bylund 2008). Clupeids contain enough thiamine concentrations for fish nutrition, but the thiaminase concentrations are problematic for the predator, causing severe degradation of thiamine reserves. Feeding on thiaminase rich fish as 100% of the diet has created decreased thiamine concentrations in eggs of lake trout, producing early mortality syndrome and diets of 35% or more can have potentially detrimental effects of natural recruitment efforts by wild lake trout (Honeyfield *et al.* 2005). Lab studies have shown it takes a minimum of two years for a depletion in egg thiamine concentrations to occur and cause the onset of early mortality syndrome while feeding on a thiaminase diet (Honeyfield *et al.* 2005). Thiaminase has been found in the spreading northern anchovy, possibly linking their high lipid content and thiaminase concentrations with thiamine deficiency in California salmonine populations (Stout *et al.* 1963, Greig and Gnaedinger 1971).

With already severe declines in salmonine populations throughout California, it is critical to understand what factors are putting these populations at further risk of becoming extirpated. TDC is an evolving issue in CCV, one which needs to be further researched and understood so its impacts can be mitigated. Conserving California's fishery is important economically, but also has embedded itself into the culture of its native people.

Figures

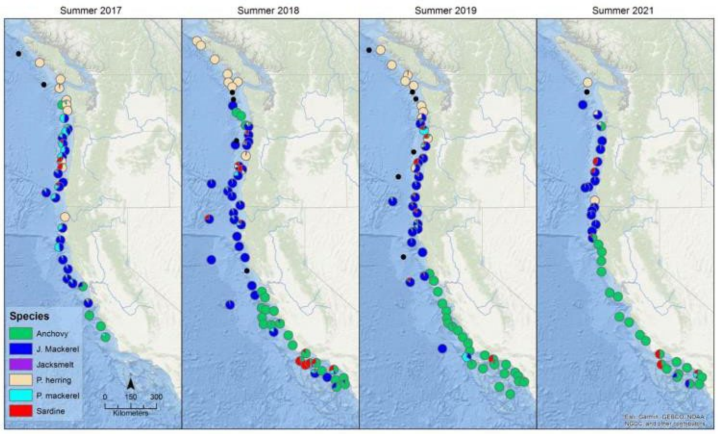


Figure 1. Proportion, by weight, of the five predominant coastal pelagic fish species (CPS) collected in nighttime trawl samples during acoustic-trawl method (ATM) surveys conducted in the California Current Ecosystem from 2017-2021 (no survey was conducted in 2020). Each pie represents a trawl cluster, which comprises up to three trawl samples per night. Black points represent trawl clusters with no CPS present. Data courtesy of Kevin Stierhoff, NOAA-SWFSC.

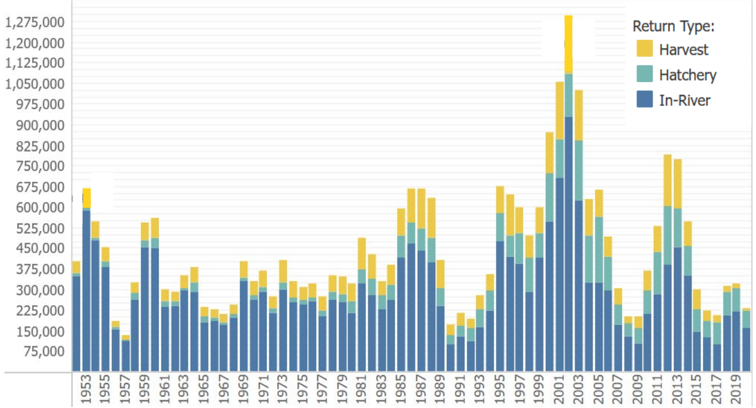


Figure 2. Yearly variations in Chinook salmon returns monitored through harvest, hatchery, and in-river estimates from 1953-2021 (Statewide Status 2021).

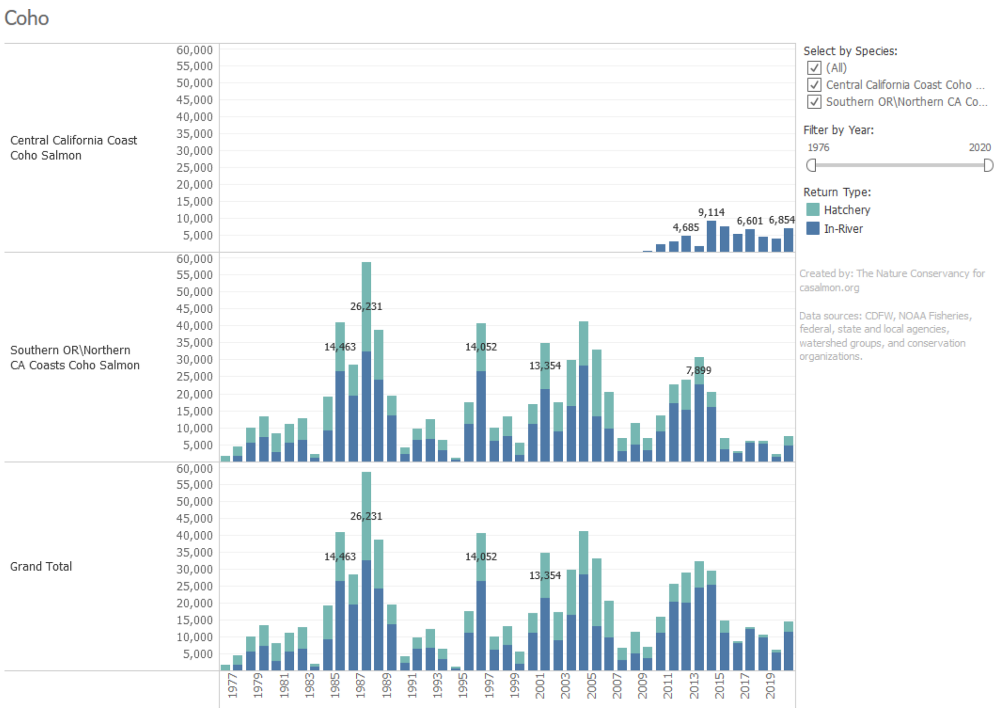


Figure 3. Abundance of adult coho salmon returns through harvest, hatchery, and in-river estimates from 1976-2020 (Statewide Status 2021).

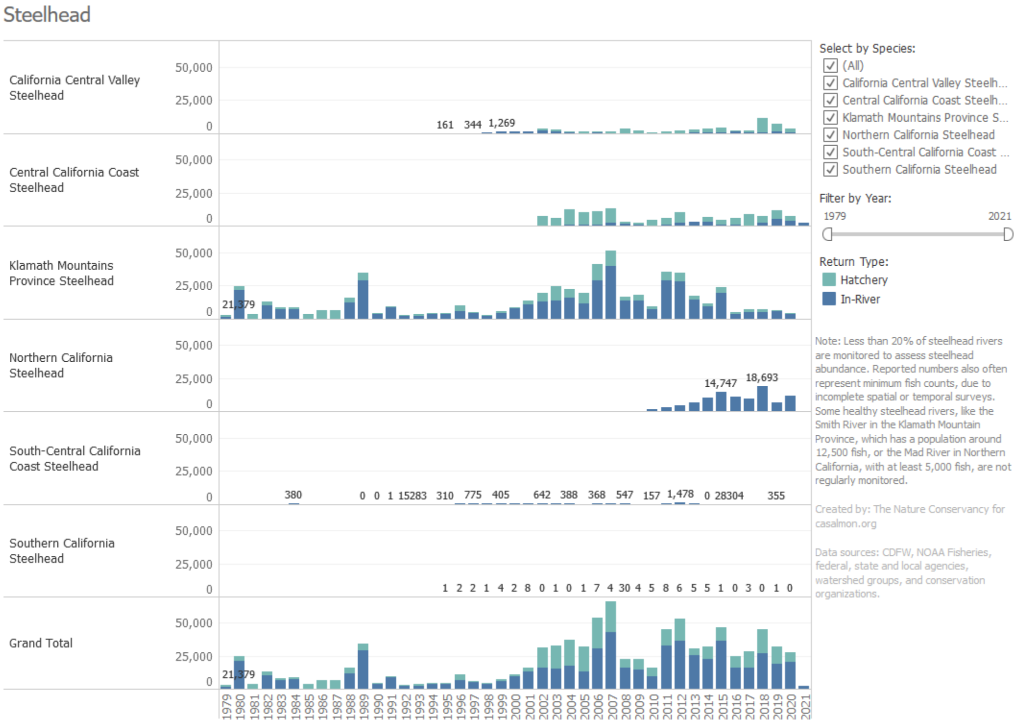


Figure 4. Abundance of adult steelhead trout returns through harvest, hatchery, and in-river estimates from 1979-2021 (Statewide Status 2021).

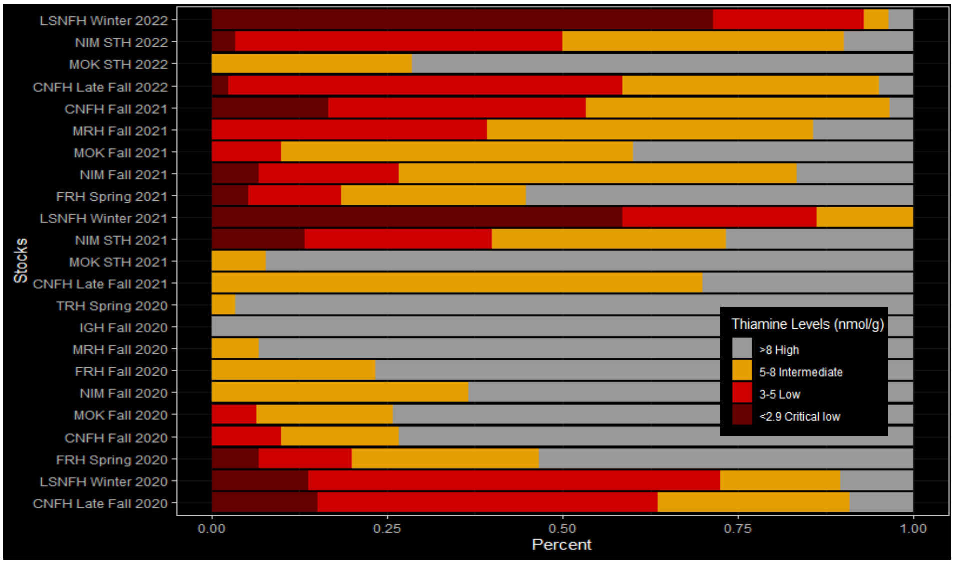
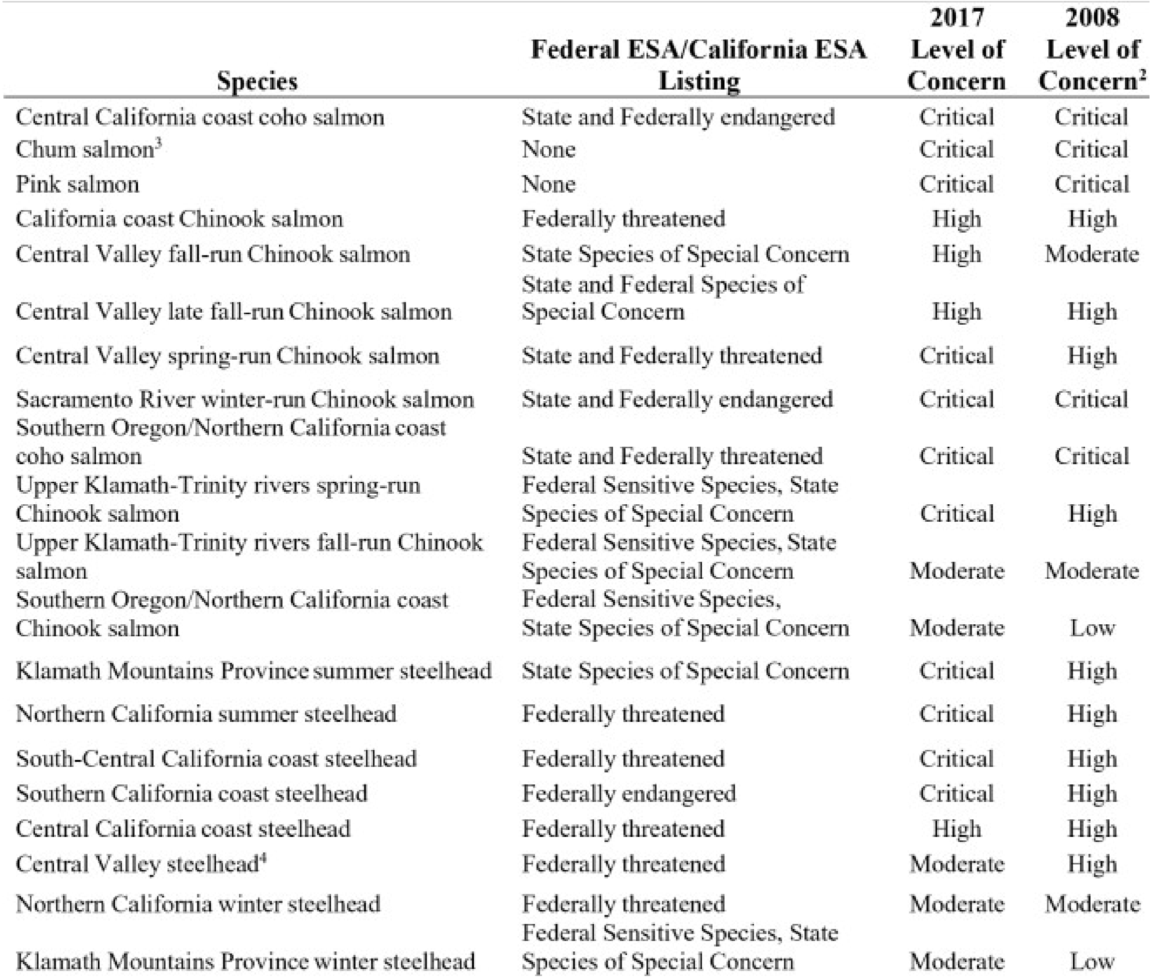


Figure 5. Thiamine concentrations of Chinook salmon in California for the California thiamine deficiency monitoring program, unpublished data by Jacques Rinchard (SUNY Brockport).

Figure 6. Hatchery locations in California's Central Valley (CCV) and Northern California. Six hatcheries are in CCV on the Sacramento and San Joaquin River systems (Livingston Stone, Coleman, Feather, Nimbus, Mokelumne, and Merced) and two hatcheries in Northern California on the Klamath and Trinity rivers (Iron Gate and Trinity).

Tables

Table 1. Listings by state and federal management agencies, status scores, and Levels of Concern for California's native salmonids, 2007 and 2017 (Moyle *et al.* 2017).



Species	Federal ESA/California ESA Listing	2017 Level of Concern	2008 Level of Concern[2]
Central California coast coho salmon	State and Federally endangered	Critical	Critical
Chum salmon[3]	None	Critical	Critical
Pink salmon	None	Critical	Critical
California coast Chinook salmon	Federally threatened	High	High
Central Valley fall-run Chinook salmon	State Species of Special Concern	High	Moderate
Central Valley late fall-run Chinook salmon	State and Federal Species of Special Concern	High	High
Central Valley spring-run Chinook salmon	State and Federally threatened	Critical	High
Sacramento River winter-run Chinook salmon	State and Federally endangered	Critical	Critical
Southern Oregon/Northern California coast coho salmon	State and Federally threatened	Critical	Critical
Upper Klamath-Trinity rivers spring-run Chinook salmon	Federal Sensitive Species, State Species of Special Concern	Critical	High
Upper Klamath-Trinity rivers fall-run Chinook salmon	Federal Sensitive Species, State Species of Special Concern	Moderate	Moderate
Southern Oregon/Northern California coast Chinook salmon	Federal Sensitive Species, State Species of Special Concern	Moderate	Low
Klamath Mountains Province summer steelhead	State Species of Special Concern	Critical	High
Northern California summer steelhead	Federally threatened	Critical	High
South-Central California coast steelhead	Federally threatened	Critical	High
Southern California coast steelhead	Federally endangered	Critical	High
Central California coast steelhead	Federally threatened	High	High
Central Valley steelhead[4]	Federally threatened	Moderate	High
Northern California winter steelhead	Federally threatened	Moderate	Moderate
Klamath Mountains Province winter steelhead	Federal Sensitive Species, State Species of Special Concern	Moderate	Low

Literature Cited

Alvarez, M. J., C. J. Lopez-Bote, A. Diez, G. Corraze, J. Arzel, J. Dias, S. J. Kaushik, and J. M. Bautista. 1998. Dietary fish oil and digestible protein modify susceptibility to lipid peroxidation in the muscle of rainbow trout (*Oncorhynchus mykiss*) and sea bass (*Dicentrarchus labrax*). British Journal of Nutrition 80:281-289.

Appert, L. 2022. Fatty acid composition in salmonid eggs – a comparative study of Atlantic salmon and brown trout. Master thesis. Swedish University of Agricultural Sciences, Uppsala, Sweden. https://stud.epsilon.slu.se/18323/.

Bell, J. G., J. McEvoy, D. R. Tocher, J. R. Sargent. 2000. Depletion of a-tocopherol and astaxanthin in Atlantic salmon (*Salmo salar*) affects autoxidative defense and fatty acid metabolism. Journal of Nutrition 130:1800-1808.

Bi, H., R. E. Ruppel, and W. T. Peterson. 2007. Modeling the pelagic habitat of salmon off the Pacific Northwest (USA) coast using logistic regression. Marine Ecology Progress Series 336:249-265.

Börjeson, H., and L. Norrgren. 1997. M74-syndrome: a review of potential etiological factors. Society of Environmental Toxicology and Chemistry, Pensacola, Florida, USA.

Burton, G. W., K. U. Ingold. 1989. Vitamin E as an in vitro and in vivo antioxidant. Annals of the New York Academy of Sciences 570:7-22.

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

Chew, B. P. 1995. Antioxidant vitamins affect food animal immunity and health. Journal of Nutrition 125:1804-1808.

Chew, B. P. 1996. Importance of antioxidant vitamins in immunity and health in animals. Animal Feed Science and Technology 59:103-114.

Chinook Salmon Species Profile, Alaska Department of Fish and Game. https://www.adfg.alaska.gov/index.cfm?adfg=chinook.printerfriendly. Accessed 7 Oct. 2022.

Copepod Populations. 2019. California Office of Environmental Health Hazard Assessment. https://oehha.ca.gov/epic/impacts-biological-systems/copepod-populations. Accessed 18 Oct. 2022.

Czesny, S., J. M. Dettmers, J. Rinchard, and K. Dabrowski. 2009. Linking egg thiamine and fatty acid concentrations of Lake Michigan lake trout with early life stage mortality. Journal of Aquatic Animal Health 21:262-271.

Daly, E. A., J. A. Scheurer, R. D. Brodeur, L. A. Weitkamp, B. R. Beckman, and J. A. Miller. 2014. Juvenile steelhead distribution, migration, feeding, and growth in the Columbia River estuary, plume, and coastal waters. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 6:62-80.

Field, J. C., A. D. MacCall, R. W. Bradley, and W. J. Sydeman. 2010. Estimating the impacts of fishing on dependent predators: a case study in the California Current. Ecological Applications 20:2223-2236.

Fisher, J., M. Trudel, A. Ammann, J. A. Orsi, J. Piccolo, C. Bucher, E. Casillas, J. A. Harding, R. B. MacFarlane, R. D. Brodeur, and J. F. Morris. 2007. Comparisons of the coastal distributions and abundances of juvenile Pacific salmon from central California to the northern Gulf of Alaska. In *American Fisheries Society Symposium*, American Fisheries Society 57:31.

Fisheries Research Board of Canada (FRBC). 1955. Pacific biological station, Nanaimo annual report. Fisheries Research Board of Canada 1954:75-106.

Fremont, L., C. Leger, B. Petridou, and M. T. Gozzelino. 1984. Effects of a (n-3) polyunsaturated fatty acid-deficient diet on profiles of serum vitellogenin and lipoprotein in vitellogenic trout (*Salmo gairdneri*). Lipids 19:522-528.

Futia, M. H., and J. Rinchard. 2019. Evaluation of adult and offspring thiamine deficiency in salmonine species from Lake Ontario. Journal of Great Lakes Research 45:811-820.

Futia, M. H., S. Hallenbeck, A. D. Noyes, D. C. Honeyfield, G. E. Eckerlin, and J. Rinchard. 2017. Thiamine deficiency and the effectiveness of thiamine treatments through broodstock injections and egg immersion on Lake Ontario steelhead trout. Journal of Great Lakes Research 43:352-358.

Fleming, I. A., and M. R. Gross. 1990. Latitudinal clines: A trade-off between egg number and size in Pacific salmon. Ecology 71:1-11.

Fowler, L. G. 1972. Growth and mortality of fingerling Chinook salmon as affected by egg size. The Progressive Fish-Culturist 34:66-69.

Gorman, A. A., I. R. Gould, I. Hamblett, and M. C. Standen. 1984. Reversible exciplex formation between singlet oxygen, $^1\Delta_g$, and vitamin E. solvent temperature effects. Journal of the American Chemical Society 106:6956-6959.

Greig, R. A., and R. H. Gnaedinger. 1971. Occurrence of thiaminase in some common aquatic animals of the United States and Canada. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Groot, C., and L. Margolis. 1991. Pacific salmon life histories. UBC Press, Vancouver, British Columbia, CA.

Halver, J. E. 1972. The vitamins. Fish Nutrition, Academic Press, San Diego, California, USA.

Halver, J. E. 2002. The vitamins. Fish Nutrition, Academic Press, San Diego, California, USA.

Hanak, E., J. Lund, A. Dinar, B. Gray, R. Howitt, J. Mount, P. Moyle, B. Thompson. 2011. Managing California's water: From conflict to reconciliation. Public Policy Institute of California.

Hatlen, B. 1997. Muscle pigmentation of arctic charr, *Salvelinus alpinus* (L.). Doctoral thesis. University of Tromso, Tromso, Norway.

Hill, K. T., P. R. Crone, N. C. H. Lo, B. J. Macewicz, E. Dorval, J. D. McDaniel, and Y. Gu. 2011. Assessment of the Pacific sardine resource in 2011 for U.S. management in 2012. https://repository.library.noaa.gov/view/noaa/4507.

Honeyfield, D. C., J. P. Hinterkopf, J. D. Fitzsimons, D. E. Tillitt, J. L. Zajicek, and S. B. Brown. 2005. Development of thiamine deficiencies and early mortality syndrome in lake trout by feeding experimental and feral fish diets containing thiaminase. Journal of Aquatic Animal Health 17:4-12.

Hoseinifar, S. H., S. Yousefi, H. Van Doan, G. Ashouri, G. Gioacchini, F. Maradonna, and O. Carnevali. 2021. Oxidative stress and antioxidant defense in fish: the implications of probiotic, prebiotic, and synbiotics. Reviews in Fisheries Science & Aquaculture 29:198-217.

Izquierdo, M. S., H. Fernández-Palacios, and A. G. J. Tacon. 2001. Effect of broodstock nutrition on reproductive performance of fish. Aquaculture 197:25-42.

Keinänen, M., A. Uddström, J. Mikkonen, M. Casini, J. Pönni, T. Myllylä, E. Aro, P. J. Vuorinen. 2012. The thiamine deficiency syndrome M74, a reproductive disorder of Atlantic salmon (*Salmo salar*) feeding in the Baltic Sea, is related to the fat and thiamine content of prey fish. ICES Journal of Marine Science 69:516-528.

Kondolf, G. M., M. G. Wolman. 1993. The sizes of salmonid spawning gravels. Water Resources Research 29:2275-2285.

Krinsky, N. I. 1993. Actions of carotenoids in biological systems. Annual review of nutrition 13:561-587.

Kuriyama, P. T., J. P. Zwolinski, and K. T. Hill. 2020. Assessment of the Pacific sardine resource in 2020 for U.S. management in 2020-2021. NOAA Technical Memorandum NMFS-SWFSC 628.

Lavaniegos, B. E., and M. D. Ohman. 2007. Coherence of long-term variations of zooplankton in two sectors of the California Current System. Progress in Oceanography 75:42-69.

Lehninger, A. L. 1970. Biochemistry: the molecular basis of cell structure and function. Worth Publishers, New York, NY, USA.

Lindley, S. 2021. Thiamine deficiency in salmonines. https://www.pcouncil.org/documents/2021/03/e-1-b-supplemental-fsc-presentation-1-thiamine-deficiency-in-salmoninds-lindley.pdf/).

Mantua, N., R. Johnson, J. Field, S. Lindley, T. Williams, A. Todgham, N. Fangue, C. Jeffres, H. Bell, D. Cocherell, and J. Rinchard. 2021. Mechanisms, impacts, and mitigation for thiamine deficiency and early life stage mortality in California's Central Valley Chinook salmon. North Pacific Anadromous Fish Commission Technical Report 17:92-93.

McCullough, D. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. Columbia River Inter-Tribal Fish Commission. A report to the U.S. Environmental Protection Agency, Seattle, WA. 291.

Merkel, T. J. 1957. Food habits of the king salmon, *Oncorhynchus tshawytscha* (Walbaum), in the vicinity of San Francisco, California. California Fish and Game 43:249-270.

Merz, J. 2002. Seasonal feeding habits, growth, and movement of steelhead trout in the lower Mokelumne River, California. *California Fish and Game* 88:95-111.

Merz, J. E., J. D. Setka, G. B. Pasternack, and J. M. Wheaton. 2004. Predicting benefits of spawning-habitat rehabilitation to salmonid (*Oncorhynchus spp.*) fry production in a regulated California river. Canadian Journal of Fisheries and Aquatic Sciences 61:1433–1446.

Milne, D. J. 1950. The differences in the growth of coho salmon on the east and west coasts of Vancouver Island in 1950. Fisheries Research Board of Canada Progress Report of Pacific Coast 85:80-82.

Morito, C. L. H., D. H. Conrad, and J. W. Hilton. 1986. The thiamine deficiency signs and requirement of rainbow trout (*Salmo gairdneri*, Richardson). Fish Physiology and Biochemistry 2:93-104.

Moyle, P. B. 2002. Inland fishes of California: revised and expanded. University of California Press.

Moyle, P. B., R. A. Lusardi, P. J. Samuel, J. V. E. Katz. 2017. State of the salmonids: Status of California's emblematic fishes 2017. Center for Watershed Sciences, University of California, Davis and California Trout, San Francisco, CA. 579 pp.

Muhs, D. R. 2018. T.D.A. Cockerell (1866-1948) of the University of Colorado: his contributions to the natural history of the California islands and the establishment of Channel Islands National Monument. Western North American Naturalists 78:247-270.

Myers, K. W. 2018. Ocean ecology of steelhead. Pages 779– 904 *in* R. Beamish, editor. The ocean ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Maryland.

NOAA Fisheries. 2022. New marine heatwave emerges off west coast, resembles "the blob". https://www.fisheries.noaa.gov/feature-story/new-marine-heatwave-emerges-west-coast-resembles-blob.

Pearcy, W. G. and J. P. Fisher. 1988. Migrations of coho salmon, *Oncorhynchus kisutch*. Fishery Bulletin 86:173.

Peterson, W. T., C. A. Morgan, J. P. Fisher, and E. Casillas. 2010. Ocean distribution and habitat associations of yearling coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon in the northern California Current: Ocean distribution of juvenile salmonids. Fisheries Oceanography 19:508-525.

Pettersson, A., Å. Lignell. 1998. Low astaxanthin levels in Baltic salmon exhibiting the M74 syndrome. American Fisheries Society Symposium 21:26-30.

Pickova, J. 1998. Lipids in cod (*Gadus morhua* L.) and Atlantic salmon (*Salmo salar* L.) eggs, with special emphasis on reproduction and quality. Dissertation. Swedish University of Agricultural Sciences Sveriges lantbruksuniv.

Riddell, B. E., R. D. Brodeur, A. V. Bugaev, P. Moran, J. M. Murphy, J. A. Orsi, M. Trudel, L. A. Weitkamp, B. K. Wells, and A. C. Wertheimer. 2018. Ocean ecology of Pacific salmon and trout: Ocean ecology of Chinook salmon, American Fisheries Society, Bethesda, Maryland, USA.

Sargent, J. R., D. R. Tocher, and J. G. Bell. 2002. The lipids. Fish Nutrition, Academic Press, San Diego, California, USA.

Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2010. State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley: Life history in managed environments. Evolutionary Applications 3:221-243.

Shapovalov, L. and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game. 98:108-243.

Silliman, R. P. 1941. Fluctuations in the diet of the chinook and silver salmons (*Oncohynchus tschawytscha* and *O. kisutch*) off Washington, as related to the troll catch of salmon. Copeia 2:80-87.

Smith, J. J. and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. Predator and Prey in Fishes, Springer Publishing, New York City, New York, USA.

Species and lifecycle: Pacific Salmon Foundation. https://psf.ca/learn/species-lifecycle/. Accessed 7 Oct. 2022.

Statewide Status – State of Salmon. (n.d.). https://casalmon.org/statewide-status/#steelhead.

Stefansson, S. O., B. T. Björnsson, L. O. Ebbesson, and S. D. McCormick. 2008. Smoltification. Fish Larval Physiology. CRC Press, Boca Raton, Florida, USA.

Stout, F. M., J. E. Oldfield, and J. Adair. 1963. A secondary induced thiamine deficiency in mink. Nature 197:810-811.

Thalmann, H. L., E. A. Daly, and R. D. Brodeur. 2020. Two anomalously warm years in the Northern California Current: Impacts on early marine steelhead diet composition, morphology, and potential survival. Transactions of the American Fisheries Society 149:369-382.

Torrissen, O. J., Hardy, R. W., and Shearer, K. D. 1989. Pigmentation of salmonids: carotenoid deposition and metabolism. CRC Critical Reviews in Aquatic Science 1:209-225.

Thayer, J. A., J. C. Field, and W. J. Sydeman. 2014. Changes in California Chinook salmon diet over the past 50 years: relevance to the recent population crash. Marine Ecology Progress Series 498:249-261.

Thompson, L. C., M. I. Escobar, C. M. Mosser, D. R. Purkey, D. Yates, and P. B. Moyle. 2012. Water management adaptations to prevent loss of spring-run Chinook salmon in California under climate change. Journal of Water Resources Planning and Management 138:465-478.

Tillitt, D. E., J. L. Zajicek, S. B. Brown, L. R. Brown, J. D. Fitzsimons, D. C. Honeyfield, M. E. Holey, and G. M. Wright. 2005. Thiamine and thiaminase status in forage fish of salmonines from Lake Michigan. Journal of Aquatic Animal Health 17:13-25.

U.S. Department of the Interior. 2008. Central Valley project and state water project operations criteria and plan biological assessment. Bureau of Reclamation, Mid-Pacific Region, Sacramento, CA.

van den Berghe, E. P., and M. R. Gross. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus* kisutch). Evolution 43:125-140.

Watanabe, T. and W. Miki. 1993. Astaxanthin: an effective dietary component for red sea bream broodstock. Fish Nutrition in Practice. INRS, Quebec City, Quebec, CA.

Willson, M. F. 1997. Variation in salmonid life histories: patterns and perspectives. U.S. Forest Service Research Paper PNW-RP-498.

Wistbacka, S., and G. Bylund. 2008. Thiaminase activity of Baltic salmon prey species: a comparision of net- and predator-caught samples. Journal of Fish Biology 72:787-802.

Yoshiyama, R., F. Fisher, and P. Moyle. 1998. Historical abundance and decline of Chinook salmon in the Central Valley Region of California. North American Journal of Fisheries Management 18:487-521.

Zimmerman, C. E., and G. H. Reeves. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning survey and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57:2152-2162.