

*Proposal submission for the
CALFED 2007 Supplemental PSP*

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Title of Supplemental Proposal: Life History Variation in Steelhead Trout and
the Implications for Water Management: Supplemental Grant Application

Funding Amount Requested: \$ 194,620

Original Proposal Title: Life History Variation in Steelhead Trout and the
Implications for Water Management

Year of Original Proposal Submission: 2004

Life History Variation in Steelhead Trout and the Implications for Water Management: Supplemental Grant Application

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Project Purpose

Our project continues to focus on understanding how stream flow levels and the patterns of water delivery in regulated rivers impact growth opportunities and life-history expression in juvenile steelhead (*Oncorhynchus mykiss*). At the end of their first year in the stream, age-0 steelhead can follow three possible trajectories: smolt transformation and emigration to the ocean, remaining in freshwater as immature parr, or maturation as residents. There is currently a lack of understanding as to how individual steelhead arrive at a particular life-history pathway. We know this decision is likely based on a combination of genetic thresholds and environmental cues, based on work done in Atlantic salmon (Mangel 1994, Thorpe et al. 1998). A better understanding of this decision process will improve our ability to monitor and predict effects of changing environments on steelhead populations in California. In addition, the increased knowledge of life-history strategies in *O. mykiss* will be very valuable to understanding the alternate pathways of anadromy and residency, which can occur in sympatry, and have direct implications for listing of steelhead populations under the Endangered Species Act. Controversy over whether to include or exclude resident fish as part of an *O. mykiss* ESU continues, although a compromise decision was reached in 2003 with the West Coast Biological Review Team's report on the 'Updated status of federally listed ESUs of West Coast Salmon and Steelhead'. Using the approach outlined in our initial proposal, we are currently conducting field studies, controlled lab experiments and modeling to examine growth patterns and life history decisions in age-0 steelhead. These processes are being compared in two Central Valley (American and Mokelumne Rivers) and two central coast (Scotts and Soquel creeks) populations.

Background and Conceptual Models (what's new)

The theoretical framework for our study is based on life-history pathways in juvenile Atlantic salmon (*Salmo salar*) and the associated conceptual framework (Mangel 1994, Thorpe et al. 1998). This species is known to have alternate life-history forms, with some fish maturing in freshwater as residents and others emigrating at various ages and becoming anadromous. This framework assumes that smolting and maturation are mutually exclusive pathways, and growth in the first year of life largely determines the pathway an individual will take. Under the theory, the fastest growing parr in a cohort should mature as residents, the next fastest should smolt the following year, and the slowest growers should remain as immature parr for another year. The decision to smolt or remain as an immature parr is governed by whether an individual reaches a genetically determined threshold size by the end of a certain time of year, or decision window.

Our study, supported by our current CALFED grant, is examining the relevance of this theory for steelhead populations in California. Consequently, we are focusing on measuring growth rates in individual steelhead, and following these individuals to determine which life-history pathway they ultimately follow. The end product of this study will be a simulation model that incorporates data on growth, survival, stream flow, and food availability to make predictions of what environmental conditions should cause a juvenile steelhead to smolt (and at what age)

and which should lead it to mature as a resident. We will develop recommendations to management regarding how patterns in water flow influence life history decisions.

Several studies on growth and life-history pathways in salmonids have recently been published which are relevant to our study. Harvey et al. (2005) investigated the relationships between habitat and density, growth and survival of juvenile steelhead during summer in a small coastal California stream. They found that high densities were positively related to depth and cover, and that growth was density dependent, positively related to depth, and increased downstream within the study reach. They suggested that dry season stream discharge was a limiting factor on growth of juvenile steelhead in this stream.

More recently, Harvey et al. (2006) examined how artificially reducing water flow to sections of a small northern California stream impacted the growth and survival of age 1 and older juvenile steelhead, with experiments conducted in summer. They found that reduced flows had very little impact on stream temperatures, and no change in survival was observed, but trout in control reaches with normal flows had over eight times higher growth rates than those in sections with reduced flows. This difference was largely attributed to a decrease in the invertebrate drift to pools in the reduced flow areas. These results reflect what we have observed on Scotts and Soquel Creeks, where growth appears to be limiting during the summer and fall when streamflow is typically very low.

Arnekleiv et al. (2006) also found significant effects of water flow on temporal and spatial variation in growth of juvenile Atlantic salmon. Over a ten year period, during which a power station was built on the river in year 5, a major part of the temporal variation was explained by mean daily discharge and spring water temperatures. They concluded that the power station caused a large increase in drift densities of zooplankton and chironomids, which was the likely reason for the higher growth rates observed just downstream.

Brook trout are a species similar to steelhead in that they also can have sympatric resident and anadromous life-history forms. A recent study of a brook trout population in Quebec examined how size at age and sex ratio varied among these two different life-history forms, and found that there was no difference in length at one year of age (Theriault and Dodson 2003). This suggests that other factors such as growth efficiency and genetics must be involved in the decision to smolt or mature as a resident. This results conflicts with one of the basic predictions of Thorpe et al. (1998); i.e. that the fastest growing juveniles tend to mature as residents, while slower growing fish become smolts.

Summary of Progress to Date (what we've learned)

Field studies - fish

Our initial results show that Central Valley steelhead have much higher growth rates than coastal steelhead, with more than a magnitude difference in growth rate between Soquel Creek and the American River (Fig. 1). Growth rates in coastal California steelhead are highest in the winter and spring seasons, and relatively slow in the summer and fall. Many fish actually lose weight over the summer and fall, when streamflow is very low and water temperatures are relatively high. This is in direct contrast to most reported growth patterns for steelhead parr in northern populations, where growth is very slow in the winter. Steelhead parr in the American and Mokelumne Rivers appear to have extremely fast growth rates year-round. Most American River steelhead achieve a length greater than 150mm FL in their first year, and many reach lengths greater than 200mm FL (Fig. 2). This is one of the fastest reported growth rates for steelhead. Stream flows and temperatures are relatively stable in the tailwater reaches of these large, regulated Central Valley rivers, potentially allowing continued rapid growth throughout the year. We have not found evidence of a bimodal size distribution of steelhead by

winter (example for one site in Fig. 3), which may be indicative of a different genetic-environment interaction in California steelhead vs. Atlantic salmon in Scotland. There are also marked contrasts between Central Valley and central coast systems in densities of juvenile steelhead and the composition of the fish community. The central coast systems have high densities of age-0 steelhead and range from complete dominance of the fish community by salmonids (steelhead only in Soquel Creek, steelhead and coho in Scotts Creek) in the upper watershed to a mix of sculpins, steelhead, and sticklebacks at low elevation sites. Central Valley communities have low densities of steelhead and a broad diversity of fishes, including many introduced species.

In the coastal streams, the resident life history of *O. mykiss* appears to be more common at the farthest upstream sites, based on recaptures of PIT tagged fish over three to four years for some individuals (Fig. 4). The sex of these individuals is often difficult to determine, though males are expected to dominate among the resident form. Resident *O. mykiss* have been documented in the Mokelumne River, and may be present in the American River.

Field studies – invertebrate prey

Understanding how stream flow levels relate to food availability is a vital component of the steelhead life-history model. To determine the abundance of prey across time, invertebrate sampling has been conducted using two methods, surber sampling for benthic invertebrates and drift nets for water column invertebrates, at all of our sites. Our results thus far suggest that drift samples provide a valid estimate of prey available to juvenile steelhead, and diel differences in drift density are minimal. Across seasons we found that the coastal streams have polymodal spikes in drift densities while the Central Valley rivers do not exhibit distinct peaks in drift in any given month, although there is a seasonal peak in late spring (Fig. 5). Overall prey availability in Central Valley rivers greatly exceeds that of central coast creeks (Fig. 6), providing a likely explanation for the remarkable difference in growth rates.

We are also addressing how invertebrate drift relates to actual diet in steelhead parr. Based on gastric lavage, we have found that steelhead from the coast and Central Valley primarily consume mayflies, caddisflies and dipterans. Other food organisms consumed by coastal steelhead included stoneflies and beetle larvae, while Central Valley steelhead consumed mites, beetles and zooplankton. A comparison of food availability and actual diet consumption revealed that food items were not consumed in proportion to their availability in the drift or benthos, demonstrating prey selectivity by steelhead.

Our analyses thus far have focused on numbers of prey items available to fish predators. Future analyses will examine how the mass of prey items changes our interpretation of the drift dynamics. This will be particularly interesting for the Mokelumne River, which contains a high abundance of zooplankton.

Lab Studies

Our lab experiments have focused on modifying growth opportunity for age-0 steelhead and determining the role of temporal variability in growth on subsequent decisions to smolt. We are comparing these effects in a Central Valley strain from Coleman National Fish Hatchery and a central coast strain from Scotts Creek. We have completed one year of the lab studies, using temperatures typical for the central coast, and are nearing completion of the second year, using temperatures matching northern Sacramento River conditions. Our results from year one indicate striking differences in growth capacity under common conditions between the two strains (Fig. 7), with fish from Scotts Creek achieving smaller sizes and showing little response to elevated food availability. We have used survival in a March seawater challenge as a proxy for determining smolting status. Initial results suggest that both strain and fish size significantly

influence seawater survival (Fig. 8), with larger fish surviving better than smaller fish, and higher survival of the Scotts Creek strain compared to the Coleman strain. The timing of the high ration period had no apparent effect on the survival of Scotts Creek fish, but since these fish had very high survival overall and showed no growth or behavioral changes during the high ration period, there would be little reason to expect a survival response. Coleman fish receiving high rations during the latest period (Jan 19-March 16) survived significantly worse than the other treatments, especially when accounting for the effects of final size. Survival rates for treatment 3 (November 23-January 18) were marginally lower as well. This suggests that growth achieved before the end of January, and possibly as early as late November, may influence whether Coleman steelhead prepare to smolt by March. We have also observed distinct behavioral differences between the two strains. In general, steelhead from Coleman were more active feeders, and spent less time hiding at the bottom of their tanks, and as noted before were the only fish to grow faster in response to elevated food supply.

One interesting finding of the lab experiment is that out of four mature males found, three survived the seawater challenge. It appears that it is at least physiologically possible for steelhead to both mature sexually and survive in the ocean.

Modeling studies

We have developed a fully functional stochastic dynamic programming (SDP) model that predicts smolting and maturity in female steelhead, given size-specific functions describing growth and survival in rivers and the ocean. While both the growth and survival models will need to be refined as field work progresses, using preliminary fits and literature values leads to prediction (verified by observation) that the vast majority of American River steelhead should smolt at age 1 while smolting occurs later for fish from central coast creeks (Mangel and Satterthwaite 2008) under current conditions. We have expanded on the predictions of Thorpe et al. (1998), noting that even extreme increases in freshwater growth rate are unlikely to lead to females adopting a resident lifestyle without very large increases in the asymptotic sizes achieved by fish in freshwater (along with very high survival and repeat spawning). We also predict (given our current best estimates of survival and seasonal variation in growth) that very slow stream growth may cause females to adopt a resident lifestyle, a pattern we may be seeing in Soquel Creek. This is a novel prediction, not anticipated by previous models.

Overall our results suggest a number of departures from the Thorpe et al. (1998) model of Atlantic salmon, representing the relatively unique evolutionary biogeography of steelhead in California. Our next set of models will allow us to more precisely frame the connection between environmental conditions and life history pathways. As our ongoing research adds more information to our datasets we hope to further refine our interpretation of the role of water flow fluctuations in determining life histories of central coast vs. Central Valley steelhead.

Approach and Scope of New Work

New components of our research will focus on three field-based goals: 1) more focused examination of fluctuations in prey availability associated with fluctuations in water flow, 2) detailed examination of movement patterns for fish in the American River, and 3) sampling in coastal lagoons to determine emigration patterns of smolts. These additional components will fill important gaps and improve the overall integration of our project.

Prey availability clearly underlies the remarkable differences in growth rates between Central Valley and central coast systems and we believe it provides the vital link between water flows and life history expression. Our ongoing invertebrate sampling program will establish

spatial patterns in prey communities across the multiple sites in each of the four stream systems, both for the benthic community (using surber samples) and the drift community (using drift nets). Preliminary comparisons of the invertebrate data and diets of steelhead obtained from gastric lavage indicate that the drift samples provide a valid index of prey availability. Diel sampling has revealed minor differences based on the time of day. These results allow us to now focus on the role of water flow. We will conduct more intense sampling at a single site in the Central Valley (on the American River) and a single site on the coast (Scotts Creek) using daytime drift samples deployed opportunistically to track the cycle of fluctuating water flow events. For the coastal site, we will conduct a series of drift sampling before, during, and after rainstorms. Water flows in creeks during major storms can increase 1000 fold, with rapid rises and falls, matching rain levels. We will sample across at least 4 of these storm events. For the American River, fluctuations in water flow are more dependent on releases from Folsom Dam. With advanced knowledge of releases we will be able to conduct a similar series of before, during, and after sampling. We will likewise sample at least 4 release events to capture the differences in prey availability associated with water flow.

Our second goal focuses on the patterns of in-stream movement and timing of emigration. We will conduct this work on the American River, where extremely fast juvenile growth rates provide the opportunity of tracking age-0 fish movement using acoustic tags. Counter to the theory of Thorpe et al. (1998), which proposes that such rapid growth rates should result in a high proportion of fish selecting early maturation and the resident life history, we believe that most of the American River steelhead emigrate after one year of freshwater residence. The large size of this river has limited our ability to acquire multiple recaptures of PIT tagged individuals. However, the growth rates achieved by age-0 fish during the summer allow us to implant the larger sized acoustic tags. We can then take advantage of the expansive existing array of hydrophones to document movement through the Sacramento River, the Delta, and San Francisco Bay out to the Golden Gate Bridge. We have obtained funding from the state to purchase 100 tags, 4 hydrophones, and associated supplies. The 4 new hydrophones will be placed along the American River, enabling monitoring of in-stream movement. Fish will be tagged in the late winter prior to expected emigration. We will attempt to tag as broad a size range as possible to allow determination of any size effect on the probability of emigration and any trend in timing of movement. Only wild fish will be tagged, allowing us to compare the behavior of wild fish with results obtained by the ongoing CALFED funded study of migration patterns in Coleman hatchery steelhead (Klimley et al.). Scales removed from all tagged fish will be used to estimate prior growth histories and determine any influence on subsequent migration patterns.

Our third goal addresses patterns of emigration in the coastal streams. We have PIT tagged large numbers of juvenile steelhead in the upper portions of our study watersheds, and will continue to do so as part of our primary project. Our recapture rates within the study sites are very high, allowing direct measurement of growth and verification of continued occurrence within the watershed. However, we do not have a viable method of distinguishing between emigration and mortality, and we do not know the characteristics of fish that survive the transition to the lagoons prior to emigration. Prior work in Scotts Creek by Hayes et al. (in press) has documented the use of lagoon habitats for extended time periods by steelhead, with markedly enhanced growth rates compared to juveniles occupying upstream habitats. We have little information on comparable estuarine residence by fish in Soquel Creek, which has a channelized stream bed and a much smaller lagoon. We propose to do extensive sampling using seines and hook-and-line gear in the estuaries of both Soquel and Scott Creek. Captured fish will

be staged (parr, silvery parr, smolt) and measured, and scales used to determine age and prior growth history. Both lagoons typically become enclosed by sandbars in late fall, when water levels drop to their annual minimum. We will sample the lagoons throughout the year but will focus our sampling efforts during this time period, when emigrating fish will be present in the lagoon but cannot leave. Growth and movement patterns of recaptured PIT tagged fish in the lagoons will be compared with those of fish remaining in upstream habitats to determine any life history factors associated with selection of the anadromous vs. resident life history.

Results obtained from the additional field sampling will be incorporated into the modeling component of our integrated project. Further progress and increased predictive power of the SDP model will depend on better specification of the growth and survival functions. The additional data on prey availability patterns will be valuable in refining our model of freshwater growth and how it is modified by water flow. Emigration data are also critically important for model validation by comparing observed smolting behavior with model predictions based on individuals' growth trajectories. Additional data acquired from acoustic tagging studies on the American River and lagoon sampling in the coastal creeks will provide valuable information on which individuals make the decision to emigrate.

Another large component of future theoretical work will be a thorough local and global sensitivity analysis of the model. It will be important to quantify how strongly each parameter of the model influences predicted behavior, and how much the sensitivity of each parameter depends on the particular values used for the whole suite of parameters. This will allow us to rank how important uncertainty is in each of our parameter estimates, identifying the most pressing data needs for future empirical work. It can also identify the environmental factors most likely to have strong effects on changes in life history. These factors will be most critical for development of management recommendations..

Relevance to the CalFed Science Program

Our research is directly relevant to the CALFED management process. Improved understanding of the factors that determine life history pathways in salmonids will be valuable in understanding how decisions regarding water flow will cascade down to influence migration timing, early maturation, and the proportions of anadromy vs. residency in ESA-listed species. Our focus is not on the direct mortality effects of water diversions, but rather the more complex and gradual process of shifting phenotypes associated with a modified environment during the freshwater nursery period. The anadromous life history of *O. mykiss* continues to decline throughout California. In the Central Valley, we suspect that part of this decline is due to a greater proportion of fish adopting the resident (rainbow trout) life history. If our main hypothesis is correct and seasonal patterns of growth shape life history decisions, modified water flows can have a major impact on salmonid populations by altering natural patterns of food delivery.

The Science Program's 2004 Call for Proposals listed the following topics relevant to decision making in CALFED, including a) life cycle models and population biology of key species, b) environmental influences on key species and ecosystems, c) relative stresses on key fish species, d) direct and indirect effects of diversions on at-risk species and e) salmonid-related projects. Our project contributes to each of these topics. One of our primary products will be a life history model for steelhead, and we are examining the role of environmental modifications, specifically in water flow, on salmonid life history trajectories. Water flow manipulations impact stressors such as temperature and food availability, which we are examining in conjunction with growth measurements. Because basic life history patterns appear to be similar across different species of *Oncorhynchus*, we believe our results will also be applicable to

understanding processes in Chinook salmon, such as early maturation. For example, Beckman et al. (2007) recently reported that increased growth rates in Sacramento River Chinook induced a higher rate of early maturation in males, consistent with the theory based on Atlantic salmon (Mangel 1994, Thorpe et al 1998). New data collection proposed here for our grant supplement will allow more refined assessment of the influence of water flow on growth opportunity by providing a more detailed examination of food delivery patterns in different systems. Our results should improve understanding of the nursery environment required to increase expression of the anadromous life history, the phenotype currently at risk under ESA designation.

New Project Staff and Qualifications

No new staff will be added to the project. We are requesting continuation of support for current project members.

CalFed Supplement Proposal
 Marc Mangel
 4/1/2008 - /10/31/2009

TASK 2	AECFT2	Year 3	Year 4	Year 5	Total
Labor		-	24,988	4,998	29,985
Benefits		-	2,499	500	2,999
Travel		-	-	-	-
Supplies		-	-	-	-
Equipment		-	-	-	-
Maintenance		-	-	-	-
Graduate fees		-	-	-	-
Indirect		-	7,146	1,429	8,576
TOTAL FOR TASK 2		-	34,633	6,927	41,560

TASK 6	AECFT6	Year 3	Year 4	Year 5	Total
Labor		6,605	74,921	8,380	89,906
Benefits		2,180	18,808	1,582	22,570
Travel		500	2,000	500	3,000
Supplies		1,000	4,000	1,000	6,000
Equipment		-	-	-	-
Maintenance		-	-	-	-
Graduate fees		-	-	-	-
Indirect		2,674	25,930	2,980	31,584
TOTAL FOR TASK 6		12,958	125,659	14,443	153,060

CalFed Supplement Proposal
 Marc Mangel
 4/1/2008 - 10/31/2009

Requested Supplement Budget Summary

	4/1/08- 6/30/08	7/1/08- 6/30/09	7/1/09- 10/31/09	Fiscal Year 5 Totals
Task #2	0	34633	6927	41560
Task #6	12328	125659	15073	153060
Total	12328	160292	22000	194620

U-05-SC-40 Budget Summary

	2/1/06- 6/30/06	7/1/06- 6/30/07	7/1/07- 6/30/08	7/1/08- 1/31/09	Totals
	Fiscal Year 1	Fiscal Year 2	Fiscal Year 3	Fiscal Year 4	
Task #1	69968	141524	82555	0	294047
Task #2	0	0	62805	85310	148115
Task #3	8165	37981	0	0	46146
Task #4	0	5021	32884	0	37905
Task #5	0	0	4657	20159	24816
Task #6	34435	53813	53813	31391	173452
Task #7	24150	57960	57960	33810	173880
Task #8	16144	38745	38745	22601	116235
Total	152862	335044	333419	193271	1014596

Adjusted Budget if this supplement is approved

	2/1/06- 6/30/06	7/1/06- 6/30/07	7/1/07- 6/30/08	7/1/08- 6/30/09	7/1/09- 10/31/09	Totals
	Fiscal Year 1	Fiscal Year 2	Fiscal Year 3	Fiscal Year 4	Fiscal Year 5	
Task #1	69968	141524	82555	0	0	294047
Task #2	0	0	62805	119943	6927	189675
Task #3	8165	37981	0	0	0	46146
Task #4	0	5021	32884	0	0	37905
Task #5	0	0	4657	20159	0	24816
Task #6	34435	53813	66141	157050	15073	326512
Task #7	24150	57960	57960	33810	0	173880
Task #8	16144	38745	38745	22601	0	116235
Total	152862	335044	345747	353563	22000	1209216

Budget and Justification

We request funding to continue salary support for an additional year for Erin Collins, the technician responsible for the analysis of food availability and diet patterns. In our initial proposal we requested 3 years of support for this position, but were required to cut the third year to meet the final budget approved by CALFED. Erin has developed extensive expertise and efficiency in analyzing field samples of prey taxa and diet samples obtained from gastric lavage of captured steelhead juveniles. A grant supplement would allow us to complete 3 full years of field sampling as originally proposed. Our preliminary results have shown a remarkable divergence between the coastal streams and the Central Valley rivers in the types and amount of prey available to the fish, as well as the seasonal pattern of prey abundance. Because food availability and consequent growth rates appear to play critical roles in determining the life history pathway selected by juvenile steelhead, continuation of the prey sampling component will greatly enhance the application of field data to our modeling efforts. Erin is also playing a critical role in implementation of the acoustic tagging project. Her continuation on the project is critical for both the invertebrate work and the tagging study. In addition, a third year of funding will allow Erin to begin the process of dissemination of results, including writing papers for publication.

We also request funding to extend salary support for 6 months for Dr. D. Swank, Dr. W. Satterthwaite, and Mr. M. Beakes. Dr. Swank is the post-doc responsible for analysis of the field and lab components of the project and Dr. Satterthwaite is the post-doc responsible for model development. It has become clear from the first 1.5 years of the project that we are collecting massive amounts of data in both the field and lab components. Additional support for Dr. Swank will allow us to complete a full 3 years of empirical data collection as planned, extend the prey sampling as noted above, conduct more focused sampling to determine movement patterns (as outlined in the description of new work) and provide time for manuscript preparation. Dr. Swank recently received funding to conduct studies of steelhead emigration in the American River using acoustic tags, a project that will ideally complement the CALFED supported components of our research. Extended support for Dr. Satterthwaite will allow completion of model development and preparation of manuscripts for publication. Both post-docs will commit to completion of a series of products providing timely dissemination of results to CALFED managers. Additional support for Mr. Beakes, the technician responsible for coordinating field sampling and conducting lab experiments, will enable us to extend the field work as outlined. Mr. Beakes will also assist with data analysis and manuscript preparation, particularly for the lab component. We are not planning additional lab studies, thereby providing time for him to conduct data analyses and writing.

A small amount of funds is also requested for travel and field supplies to permit continued and extended field sampling for invertebrates in the four systems, as well as extended collections of fish for examination of movement patterns.

Literature Cited

- 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.
- Beckman, B. R., B. Gadberry, P. Parkins, K. A. Cooper, and K. D. Arkush. 2007. State-dependent life history plasticity in Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*): interactions among photoperiod and growth modulate smolting and early male maturation. *Canadian Journal of Fisheries and Aquatic Sciences* 64:256-271.
- Harvey, B.C., R.J. Nakamoto, and J.L. White. 2006. Reduced Streamflow Lowers Dry-Season Growth of Rainbow Trout in a Small Stream. *Transactions of the American Fisheries Society* 135:998-1005.
- 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, E. V. Freund, J. J. Smith, E. C. Anderson, A. J. Ammann, and R. B. MacFarlane. In press. Steelhead growth in a small Central California watershed: upstream and estuarine rearing patterns. *Transactions of the American Fisheries Society*.
- Mangel, M. 1994. Climate change and salmonid life history variation. *Deep Sea Research, II (Topical Studies in Oceanography)* 41:75-106
- Mangel, M. and W. Satterthwaite. In press. Combining Proximate and Ultimate Approaches to Understand Life History Variation in Salmonids with Application to Fisheries, Conservation and Aquaculture. *Bulletin of Marine Science*
- Theriault, V. and J.J. Dodson. 2003. Body Size and the Adoption of a Migratory Tactic in Brook Charr. *Journal of Fish Biology* 63: 1144-1159.
- Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* 12:581-599.

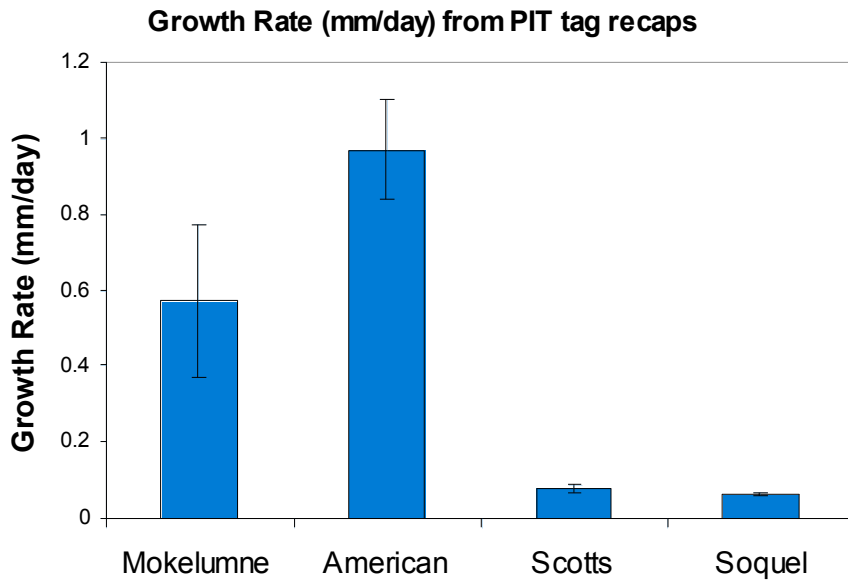


Fig. 1. Average yearly growth rates for juvenile steelhead in the four study streams, based on measurement from recaptured PIT tagged fish.

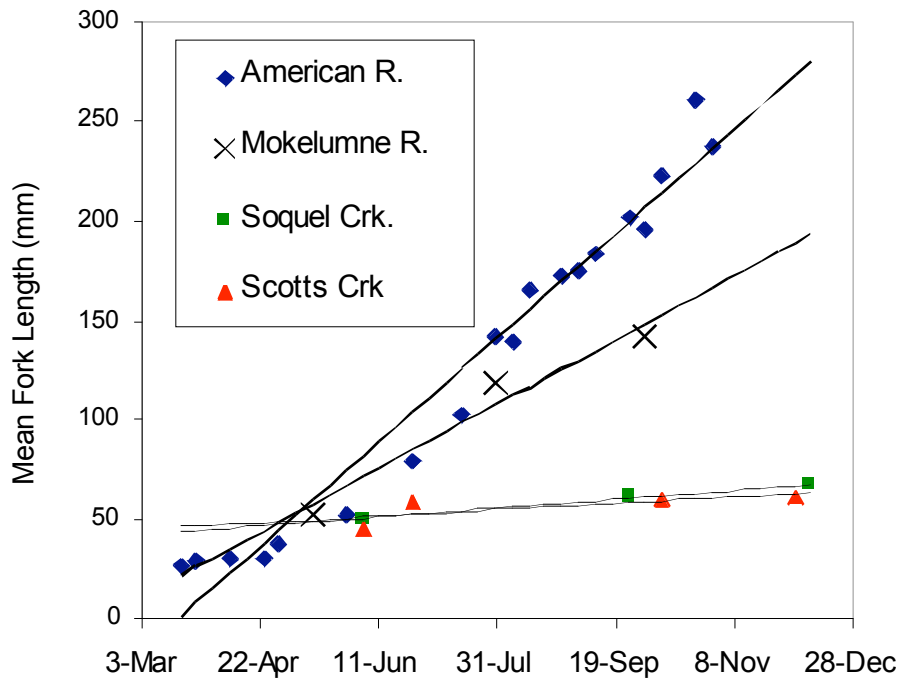


Fig. 2. Observed growth trajectories of juvenile steelhead in the four study streams, based on data from PIT tagged fish and length frequencies over the course of 2007.

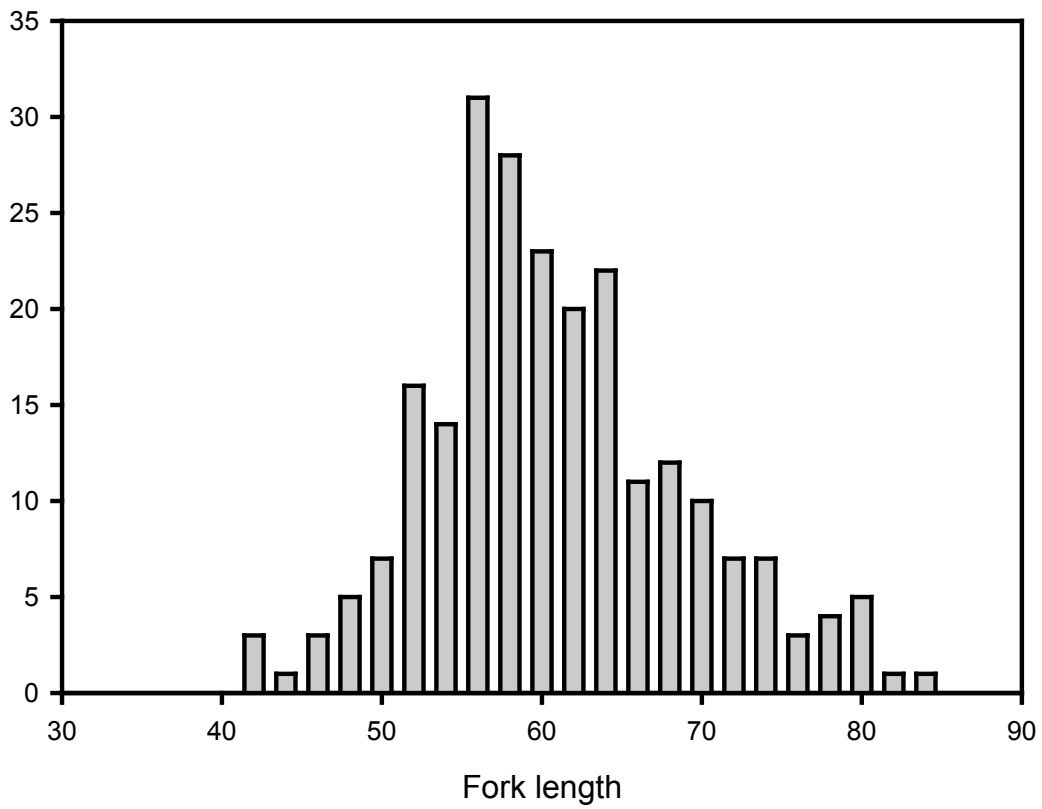


Fig. 3. Size-frequency distribution of age-0 steelhead captured in December, 2006 at the Swanton Bridge site of Scotts Creek.

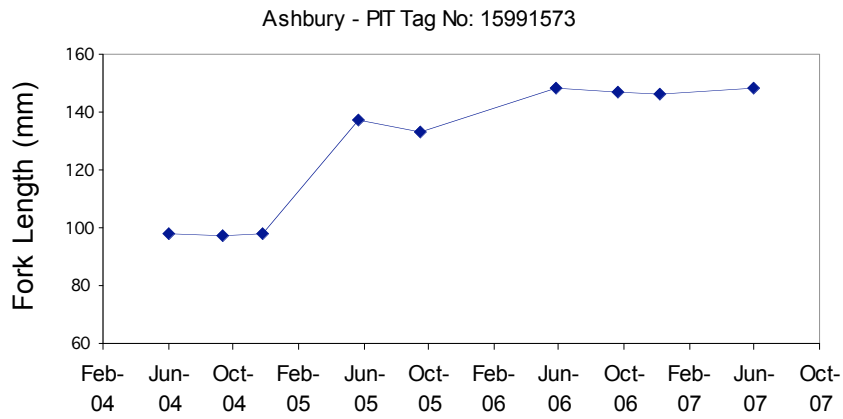


Fig. 4. Length at capture of a presumed resident steelhead from Soquel Creek. This individual was age-2 at first capture, and gained only 50mm over three years.

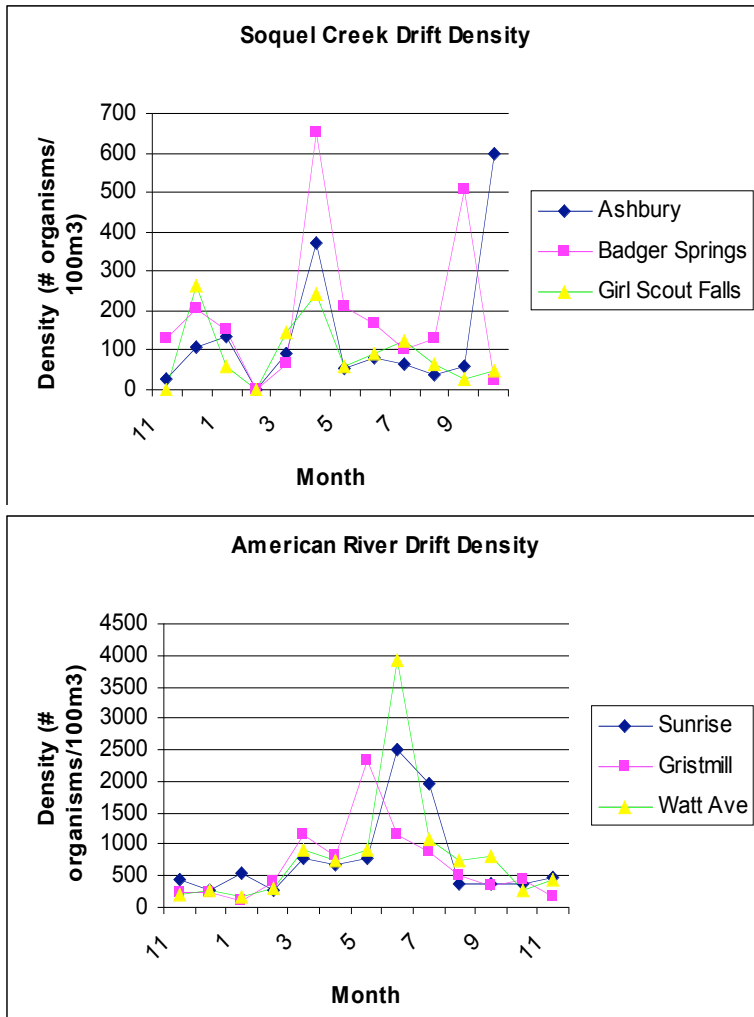


Fig. 5. Density of invertebrates caught in drift nets on Soquel Creek and the American River, in monthly samples from 2006-2007.

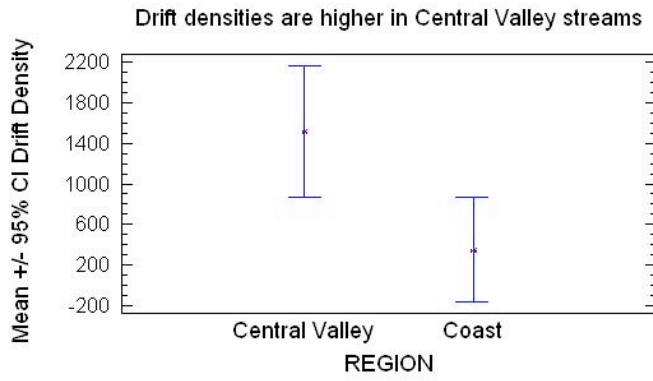


Fig. 6. Mean density of invertebrate prey collected in drift samples in Central Valley rivers (American and Mokelumne) and central coast creeks (Scotts and Soquel).

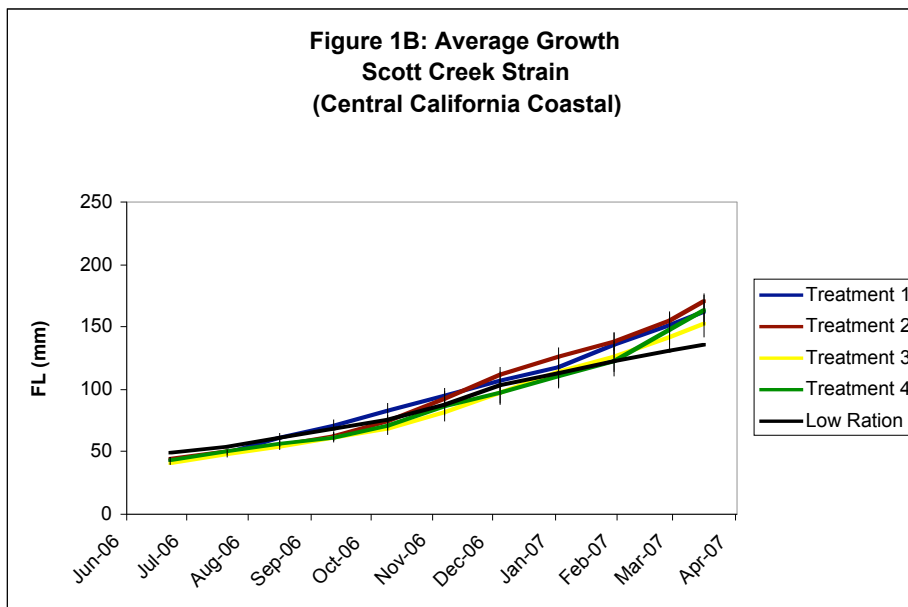
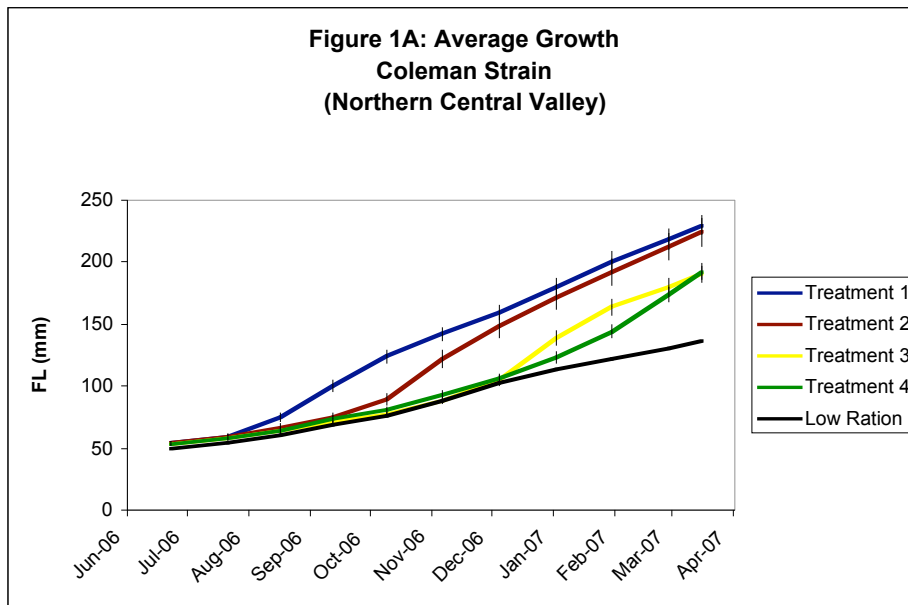


Fig. 7. Changes in growth for the two strains of steelhead over the course of four high treatment periods. A) Coleman strain fish responded strongly to a high ration period. B) Scotts Creek strain steelhead did not show any significant increase in growth rate with high rations, and had significantly reduced growth compared to Coleman fish.

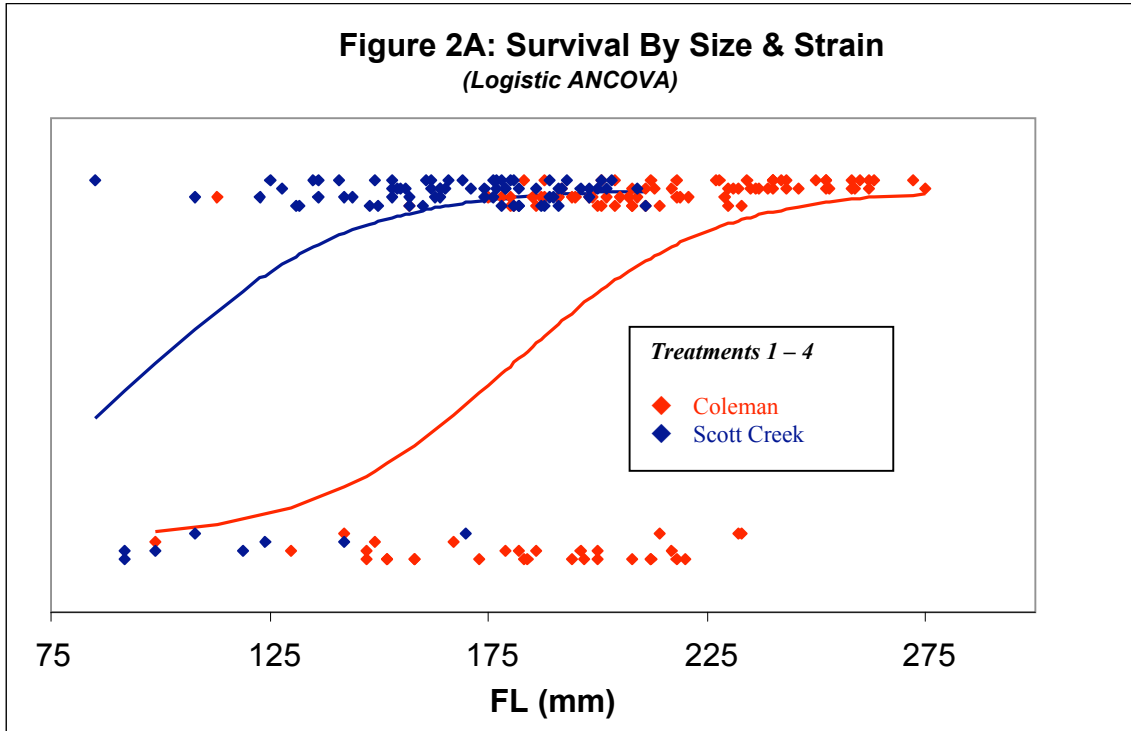


Fig. 8 Logistic regression (ANCOVA) results showed that Scott Creek strain steelhead needed to be approximately 150mm to have a 50% chance of surviving seawater challenge, while Coleman strain steelhead required a minimum size of approximately 220mm to have a 50% chance of survival. Seawater challenge survivors are the upper row of points, mortalities are the lower row. The x-axis gives the fork length of each fish at start of the seawater challenge.