FINAL REPORT, JULY - DEC, 2010

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PROJECT TITLE: LIFE HISTORY VARIATION IN STEELHEAD TROUT AND THE IMPLICATIONS FOR WATER MANAGEMENT

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Brief Description of the project: In this project, the factors determining the timing of emigration in juvenile steelhead and the role of environment, particularly water flows, in shaping this behavior are being investigated. The goal is to provide information that will help shape water policies conducive to the recovery of steelhead trout.

Primary Objective to be Achieved: To understand the factors that shape steelhead smolting and migration, a number of objectives are involved: 1) Developing a conceptual framework for steelhead life history that accounts for the relatively unique biogeography of California. 2) Making the framework into a computation tool and studying predictions that emerge from this modified framework. 3) Determining the information that size distributions and growth rate provide about the probability of migration.4) Assessing how coastal steelhead differ from Central Valley steelhead in these regards; that is, is there evidence for local adaptation or developmental plasticity? 5) Determining the implications of these results for the effects of water flows on steelhead survival and

migration. These topics are addressed from approaches of field studies, lab experiments, and modeling.

BUDGET SUMMARY

Because of the size of this project, it is not possible to insert a budget table here. The attached spreadsheet (Mangel CalFed Budget Summary) provides the overall summary and then a breakdown by task.

FINAL PROJECT STATUS (BY TASK)

TASK 1: Extend the theory of Thorpe et al. to account for steelhead in California and parameterize the models with data collected during the empirical work. This task has been completed.

Summary: We developed a stage-dependent life history model for female steelhead using the theory of Thorpe et al. (1998) as a starting point. The theory proposes that life history expression is a function of the interaction between a genetic threshold and the environment encountered by an individual. If a threshold is met at a particular time period or decision window, a physiological trigger induces the processes necessary to adopt a given life history pathway. Steelhead are similar to Atlantic salmon, the species for which the theory was developed, in their diversity of life history types and their potential for iteroparity, suggesting some commonality appropriate to the theory. However, California systems differ markedly from Atlantic salmon habitats in climate and other environmental factors likely to influence both the genetic thresholds and how those thresholds are triggered. Likewise, the extreme environmental differences between California's Central Valley and central coast suggest comparable variance in life history responses by local populations.

Our model explores the trade-offs experienced by a female steelhead at each stage in her life history, with a focus on size-dependent fecundity (favoring rapid growth and anadromy), size-dependent early marine survival (favoring a delay in emigration from freshwater), and spatial variability in freshwater growth and survival (favoring residency in some systems). The state-dependent approach allowed us to designate decision windows, during which an individual assesses its current and future state (size, growth rate, condition, etc.) and commits to a particular pathway, such as emigration at age 1.

We combined proximate (physiological) and ultimate (expected reproductive success) considerations to generalize the notion of a threshold size for emigration or maturity through the development of a state-dependent life history theory. The model involves strategies that depend on age, size or condition, and recent rates of change in size or condition during specific periods (decision windows) in advance of the actual smolting or spawning event. We used stochastic dynamic programming to identify the optimal developmental pathways for a female steelhead. Fish were assumed to adopt the optimal strategy at each decision point, based on their state, and to remain committed to that pathway.

TASK 2: The theory developed in Task 1 will be tested through experimental and observational studies. This task has been completed.

Summary: We applied the model derived in Task 1 to coastal systems, using our empirical results from Soquel and Scott Creeks, and to Central Valley rivers, using our

data from the American and Mokelumne Rivers. For the coast, we used the model to predict the combinations of emergence date and growth rate that would result in maturation at age 0. For the combinations likely to occur in the wild, only very early emergers with very fast growth rates were predicted to mature. We also modeled the age 0 smolting decision based on fish size at the end of December and their growth rate during the presumed decision window. In coastal creeks, the observed sizes and growth rates were all too low to predict emigration the following spring. By age 1, in contrast, a large proportion of the females were predicted to emigrate in spring, although the smaller, slower growers were predicted to spend another year in freshwater. With regard to maturity, the model predicts that the advantages of a large size achieved in the ocean outweigh the advantages of maturation at a smaller size in freshwater; thus, none of the observed age 1+ sizes and growth rates predicted maturation in the stream.

We also explored how changes in growth rates, as might be expected under environmental shifts in climate, would affect model predictions. Faster growth is predicted to result in a greater proportion of females smolting at younger ages, with the opposite effect predicted if growth rates are reduced. Very large changes in growth would be necessary to shift the balance between residency and anadromy for coastal female steelhead. Very fast growth is predicted to favor maturity in freshwater only if the maximum size attainable is much larger than currently observed in coastal systems. However, reduced marine survival is predicted to result in higher proportions of fish adopting the resident life history. We predict that evolutionary responses to changes in survival may be slower than plastic responses to changes in growth rate.

Overall our approach to modeling steelhead life histories shows considerable promise in explaining the existing patterns of life history variation and may be useful in predicting responses to environmental changes. Over the short term, we predict altered growth rates will most likely change life history trajectories, particularly age at smolting. Over the long term, it appears that survival probabilities, particularly in the marine environment, are most important in selecting for residency versus anadromy.

For the Central Valley systems, we developed a similar model parameterized with our results from sampling in the American and Mokelumne Rivers and addressed the life history changes that might be associated with shifts in climate or changes in flow management. The model predicted a larger threshold size for smolting for both Central Valley streams than for the coast. The modified model successfully predicted the observed pattern of complete anadromy and emigration at age 1 for the American River and the mix of strategies observed on the Mokelumne River. A relatively large proportion of older females were predicted to mature in freshwater and remain as residents in the Mokelumne, whereas fish in the American were predicted to smolt and emigrate at age 1. A comparison of relative fitness of the resident vs. anadromous life history in each system suggested a wide disparity favoring anadromy on the American, but minor differences for the Mokelumne, potentially favoring a mix of strategies to cope with a varying environment.

We advanced the management utility of this framework by explicitly modeling growth as a function of environmental conditions and using sensitivity analyses to predict likely evolutionary endpoints under changed environments. We concluded that the greatest management concern with respect to preserving anadromy is reduced survival of emigrating smolts, although large changes in freshwater survival or growth rates are potentially also important. We also demonstrate the importance of considering asymptotic size along with maximum growth rate.

TASK 3: Conduct lab experiments designed to determine the influence of growth patterns on life history decisions at age 1 in juvenile steelhead under a warm temperature regime. This task has been completed.

Summary: We obtained juvenile steelhead from Coleman National Fish Hatchery and the Monterey Bay Salmon and Trout Project hatchery (Scott Creek population) in May of 2006 and raised them under variable feeding regimes in the laboratory through March of 2007. Fish received low rations except during the treatment period, when they received eight continuous weeks of rations ad libitum daily. There were four different treatment periods progressing in time from August to March. Our objective was to provide fish with a diet supporting moderate but restricted growth except for an 8-week period of rapid growth opportunity. Temperatures were adjusted to provide a normal seasonal cycle, but under a relatively warm regime (minimum of 10°C in winter and maximum of 17°C in summer). In March all fish were subjected to a saltwater challenge to determine their life history decision of emigrating or remaining in freshwater for a second year.

The results revealed a striking difference between the two populations in both growth capacity and seawater readiness. Coleman steelhead grew at much faster rates than Scott Creek fish held under the same treatments. Scott Creek fish had much higher survival rates (91%) in seawater than Coleman fish (77%). Within each population, survival in seawater was strongly related to fish size, with larger individuals more likely to survive. However, at a given size, fish from Scott Creek were more likely to survive than Coleman fish, consistent with model predictions. Although there were slight differences in survival among the four feeding treatments, particularly for the Coleman fish, in general the timing of when fish could accelerate growth did not appear to have a strong effect on their decision to emigrate or stay in freshwater.

Although we did not observed a clear treatment effect, for both populations there was a divergence in growth rates between eventual challenge survivors and eventual mortalities very early in the experiment, with faster growth by fish adopting the emigration pathway and slower growth by those electing to remain in freshwater. Significant differences between eventual smolts (saltwater survivors) and nonsmolts (saltwater mortalities) in both size and growth rate started in summer and continued throughout the experiment for both populations. Eventual smolts from the Coleman population had lower condition factor (consistent with streamlined smolt morphology) every month after October, although this difference was not always statistically significant. A very low number of nonsmolts among Scott Creek fish precluded meaningful comparisons. This divergence does not allow us to determine a specific time window for the life history decision but does indicate that the decision occurred before the onset of winter.

TASK 4: Conduct lab experiments designed to determine the influence of growth patterns on life history decisions at age 1 in juvenile steelhead under a cool temperature regime. This task has been completed.

Summary: We obtained juvenile steelhead from the two hatchery populations in May of 2007 and raised them in the laboratory through March of 2008. Treatments were identical to the 2006 cohort but with a cooler temperature regime (minimum of 6°C in winter and maximum of 14°C in summer). In March all fish were subjected to a saltwater challenge. Differences between the two populations in terms of growth and survival in seawater challenges were similar but more subtle than observed for the 2006 cohort. Coleman steelhead continued to grow at faster rates than Scott Creek fish, but the cooler temperatures restricted their growth to overall moderate rates and the contrast

between populations was reduced. Coleman fish appeared to take advantage of the enhanced growth opportunity of warmer temperatures to a far greater extent than the Scott Creek fish, suggesting a risk prone vs. a risk averse behavioral strategy. Likewise, the difference in seawater survival between the two populations was minor (68% for Scott Creek and 59% for Coleman). The reduced survival rate compared to the 2006 cohort was potentially a function of the slower growth rates and smaller sizes of fish at the time of the seawater challenge.

As seen in the 2006 cohort, there was a slight but non-significant effect of the feeding treatment, which varied the timing of a 4 week period of accelerated growth, on the life history decision of preparation for saltwater. Also similar to the 2006 cohort, there was an early divergence in growth rates between eventual smolts and eventual non-smolts, demonstrating that initial growth advantages were maintained throughout the experiment. In addition, the 2007 cohort exhibited a switch in condition factor for fish in the two life history pathways. Eventual smolts were initially higher in condition than eventual nonsmolts, but by December this pattern was reversed and smolts had lower condition indices than non-smolts. This pattern matched the expected morphological transition associated with subsequent smolting.

The apparent timing of the decision window, several months before the typical period of smolt emigration, matches the patterns observed for other salmonids. In coastal California, this decision must occur before fish have had the opportunity to take advantage of improved winter–early spring feeding conditions. These results support the role of early growth opportunity in life history decisions and provide insight into the applicability of life history models for managing California steelhead.

TASK 5: Conduct laboratory experiments to define the timing of the maturation decision window. This task has been completed

Summary: In 2008 we again conducted laboratory experiments with Coleman and Scott Creek steelhead populations but altered the feeding treatments to potentially enhance the incidence of early maturation in males. Our hypothesis was that continual accelerated growth opportunities should lead to a greater proportion of males electing to mature at age 1 and forego emigration to the ocean altogether. In this experiment we maintained fish on ad libitum rations and varied the time at which we switched them to a restricted ration. Once on this reduced ration, their growth rates were constrained for the remainder of the experiment. We used four treatments, with fish put on reduced rations starting in August, October, December, or remaining on high rations throughout the experiment. In March we subjected the fish to a seawater challenge and examined all fish for evidence of maturity.

As in the 2006 and 2007 experiments, Coleman fish demonstrated a greater capacity for growth than the Scott Creek fish, with the treatment receiving high rations throughout the experiment attaining a mean size 75% larger than that of the treatment placed on low rations in August. For the Scott Creek strain, this difference was only 40%. Growth rates overall were much higher than would occur under natural conditions, particularly for the treatments maintained on high rations for longer periods of time. However, despite providing what we expected to be ideal conditions for selection of an early maturation pathway, the proportion of mature males in the 2008 experiment did not differ from the prior two experiments. Among the 3 years the mature males constituted 1.6, 2.2, and 2.5% of the total, with no difference between the two strains of Coleman and Scott Creek. Assuming a 50/50 sex ratio, only about 3-5% of the males made this maturation decision. With the low number of males that matured at age 0, it was not

possible to determine if the different ration treatments had a significant effect on this life history decision.

An additional hypothesis that the early maturers would be the largest fish was also not supported. At the time of the seawater challenges, mature males were generally intermediate in size between smolt (challenge survivors) and non-smolts (challenge mortalities). However, for the Scott Creek strain there was some evidence that males that matured early had faster growth rates at the beginning of the experiment than those that did not mature.

Overall our results demonstrate that the propensity for early maturation in these two populations is very low and is not determined solely by a specific size threshold during a temporal decision window. In each of the three experiments, fish were held in groups of 20 in separate tanks. At the conclusion of experiments there was never more than one mature male present in a tank, suggesting that social factors may also play a role in selection of this pathway.

Gill enzyme assays of Na+K+ATPase were conducted for all fish in each experiment during the final measurement prior to seawater challenges to evaluate its utility as a predictor of seawater readiness. The results indicated another intriguing contrast between the two strains. For Scott Creek fish there was a clear elevation of ATPase for individuals that selected the emigration pathway and survived the seawater challenge, compared to the non-smolts. Thus, this strain followed the expected pattern of elevated ATPase for smolts. Coleman fish, in contrast, did not exhibit a clear difference between smolts and non-smolts at the time of introduction to seawater. However, by again measuring ATPase levels in survivors at the end of the challenge we were able to demonstrate that Coleman fish were able to markedly increase production of ATPase once they entered seawater. For both strains, ATPase levels in mature males were very low, confirming their non-emigrating decision.

TASK 6: Field estimates of juvenile steelhead densities. This task has been completed.

Summary: Shallow depths and generally low flows in the small coastal systems allowed us to derive quantitative estimates of fish density. For Soquel and Scott creeks, we conducted electroshock sampling in June, October, and December of 2006 and 2007, and June of 2008. Depletion sampling with 3 passes provided density estimates at 4 sites in each watershed, ranging from with a few km of the ocean to near the upper limit of steelhead occurrence in each watershed. Density estimates for a 100m section of coastal stream varied from 10 to 1000 steelhead, demonstrating the range of variation depending on site, season, and year. Differences among the sites within each creek were consistent across years but did not suggest definitive upstream vs. downstream trends. Quantitative sampling was not possible in the larger rivers of the Central Valley. We used a variety of methods to capture fish in the American and Mokelumne Rivers, and supplemented our efforts with previous collections by the East Bay Municipal District and California Fish and Game. We conducted seining, boat electroshock fishing, and hook and line fishing at 3 sites on the American and 2 sites on the Mokelumne. Sampling was conducted on an opportunistic basis throughout the 3 years of this project.

Striking differences were evident in the size-frequency distribution of steelhead between the Central Valley and central coast streams, as well as between the two rivers within the Central Valley. With the exception of a single site on Soquel Creek that is above an intermittent migration barrier (Ashbury), the coastal sites were highly dominated by age-0 fish of relatively small size. A few immature, larger fish were present at each site, along with a low proportion of mature males. Steelhead in the American River comprised a single year class, with no evidence of fish older than age-0.

Following the expected timing of smolt emigration in spring, no captures of older fish occurred, suggesting that a second year of freshwater residence was extremely rare in this system. Likewise, no mature males were captured, suggesting this life history pattern was also rare. In the Mokelumne River, in contrast, a broad range of sizes was captured throughout the year, with older fish (ages 1 to 4+) often outnumbering the age 0 cohort. Large mature males were common, as well as presumed mature females, all with the morphology and coloration of resident *O. mykiss*.

These results clearly demonstrate a marked contrast in life history expression among the streams. Coastal streams are largely represented by immature fish that are likely the progeny of anadromous parents. Age 1 fish are present but in much lower numbers than age 0 fish, suggesting either high overwinter mortality or high rates of emigration at age 1. The latter is unlikely due to the small size and poor survival probability of age 1 emigrants. Fish aged 2 and older are also present, but may be represented largely by early maturing males, which then remain in the stream. At one site on Soquel Creek that has an intermittent barrier to migration, the steelhead community is comprised of a wide range of sizes and multiple recaptures over several years suggests a large proportion of resident fish. On the American River, the steelhead population consists of a single cohort, with all members emigrating after their first winter, at age 1. Extremely rapid growth rates (see below) result in a large size at the time of emigration, with a much greater likelihood of survival in the marine environment compared to age 1 fish in the coastal populations. The Mokelumne River steelhead displayed a diverse array of life history pathways, with a large proportion of residents as well as future emigrants that presumably remained in freshwater for more than a year.

TASK 7: Field estimates of invertebrate prey densities. This task has been completed.

Summary: We used surber sampling to identify and quantify prey communities in benthic habitats at each site in the four study streams. Drift nets were used to quantify prey arriving in the water column at each site. Surber sampling was conducted seasonally and drift sampling was conducted monthly over a two year period. To determine the types of prey consumed by steelhead at each site and their selectivity of different prey taxa, we conducted gastric lavage of live fish in conjunction with our regular fish collections.

There were several interesting differences in the abundance and composition of available prey among the four systems. Because the diet was comprised largely of drift organisms our analysis focused on that community rather than the benthic component collected by Surber samplers. For the American River and Scott and Soquel Creeks, the drift was dominated by organisms of benthic origin, with Chironomids typically the primary taxa. The drift community on the Mokelumne, in contrast, was dominated by pelagic Cladocerans (Daphnia in particular), presumably arriving from the reservoir above Camanche dam.

Densities of prey available in the drift were very similar for the two coastal systems and very low (overall mean of ~200 prey per 100 m^3 of water) compared to the Mokelumne (mean ~2000 prey per 100 m^3) and American (~800 prey per 100 m^3) Rivers. The extremely high density of drift organisms in the Mokelumne was a consequence of the abundance of Daphnia delivered from the reservoir habitat.

Based on the types of prey found in fish stomachs, the diet differed greatly by stream. For American River fish, 78% of the diet was comprised of Ephemeroptera and 16% by Trichoptera, with minor contributions from other taxa. In contrast to the diet, the drift community in the American River was dominated by Diptera, which comprised 43% of the available prey; Ephmeroptera contributed only 13% of the drift. Thus, the

steelhead in the American demonstrated a high level of selectivity of prey. In the Mokelumne, the drift was dominated by Cladocera (76%), followed by Diptera (11%). The diet of Mokelumne steelhead was also dominated by Cladocera but at a lower percentage (43%), and Diptera comprised 21% of the diet. For the coastal systems, the diet was more varied and less selective than in the Central Valley systems, with representation by a broad variety of taxa.

Seasonal patterns in the drift also varied between the two regions. Drift in the regulated Central Valley rivers peaked in spring and summer and was lowest during fall and winter, whereas drift in the unimpaired coastal creeks peaked during winter, spring, and fall and was lowest during summer. Drift densities were influenced by both flow and biology. High flow rates typically delivered more prey organisms to our sites, but drift densities could also be high when flows were low, presumably due to biological cycles of reproduction and emergence.

TASK 8: Natural growth variability in juvenile steelhead. This task has been completed.

Summary: We used Passively Induced Transponder (PIT) tags to individually mark steelhead. All fish captured that were > 65 mm FL were injected with a tag. Subsequent recaptures allowed us to directly estimate individual growth rates. Recaptures at the 8 coastal sites were common and provided a wealth of information on growth patterns. For the Central Valley systems, we supplemented our recaptures with additional data from EBMUD and CDFG for the Mokelumne and American Rivers respectively. In addition, we evaluated growth rates based on the progression of length frequencies over time. This method is indirect and influenced by selective mortality and variation in age composition if cohorts overlap in size. Therefore, we used it only for age-0 fish, which generally comprised a discrete mode compared to older fish.

Both methods of growth estimation revealed marked differences between the Central Valley and central coast systems. For age 0 fish, growth rates in the Central Valley were 2 to 3 times greater than those on the coast. The two regions also differed in seasonal patterns of growth. We divided growth data into two seasons for comparison, winter/spring and summer/fall. On the coast, growth rates were highest in the winter/spring, presumably due to the greater delivery of prey items associated with rain-induced increases in flow rates. In the Central Valley, growth rates were higher in summer/fall, again potentially due to the higher abundance of invertebrate prey in summer months compared to the winter. On the coast, growth rates based on recaptured fish with PIT tags were similar between the two systems of Soquel and Scott Creeks, with overall average growth in length of 0.06 mm d^{-1} in summer/fall and 0.19 mm d^{-1} in winter/spring. On the Mokelumne River growth rates of age 0 PIT-tagged fish averaged 0.81 mm d^{-1} in summer/fall and 0.44 mm d^{-1} in winter/spring. For the American River we did not have recaptures in winter, but summer growth rates of age 0 tagged fish averaged 0.98 mm d^{-1}. Analyses using length frequency data of age 0 fish produced similar rates, with an overall average of 0.12 mm d^{-1} in summer/fall and 0.22 mm d^{-1} in winter/spring for the two coastal systems, 0.64 mm d^{-1} in summer/fall and 0.51 mm d^{-1} in winter/spring on the Mokelumne, and 1.26 mm d^{-1} in summer/fall and 0.51 mm d^{-1} in winter/spring on the American. Growth rates of age 0 fish on the American River are among the highest known for steelhead throughout their range. Although the Mokelumne River had higher quantities of drifting prey than the American River, the prey available on the American were potentially of higher quality, contributing to the extremely fast growth rates observed. The absence of older age classes of steelhead on the American also eliminated the suite of potential competitors that was abundant on the Mokelumne.

Growth rates of older fish were also calculated using recaptures of PIT tagged fish for the two coastal streams and the Mokelumne (older fish did not occur on the American). On the coast, growth rates of older fish were similar to those of age 0 fish, with overall means of 0.04 mm d^{-1} in summer/fall and 0.17 mm d^{-1} in winter/spring. On the Mokelumne, older fish displayed a marked decrease in growth compared to the age 0 cohort, with means of 0.20 mm d^{-1} in summer/fall and 0.14 mm d^{-1} in winter/spring. A decline in growth would be expected for fish maturing in the river and devoting energy to reproduction.

Disposition of Funds for Supplies and Expenses: During the final period of the contract, Cynthia Kern and Noah Parker worked on and completed Tasks 3 and 4. Kern and Parker, as well as Neosha Kashef and David Stafford, completed Tasks 5, 7, and 8. Supplies were purchased for analysis of invertebrates and gill enzyme assays.

PROJECT-WIDE STATUS

ACHIEVED OBJECTIVES, FINDINGS, AND CONTRIBUTIONS: All objectives for the project have been achieved: the framework for modeling the life history of steelhead in California and the statistical methods needed for analysis of field and laboratory data have been completed, field sampling in the Central Valley and Central Coast has been completed and the three years of laboratory studies have been completed.

PROBLEMS OR DELAYS ENCOUNTERED: None

DELIVERABLES:

Papers in peer-reviewed scientific journals:

Beakes, M.P., Satterthwaite, W.H., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M. and M. Mangel. 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. Transactions of the American Fisheries Society 139:1263–1275.

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. Evolutionary Applications 3:221-243.

Satterthwaite, W.H., M.P. Beakes, E.M. Collins, D.R. Swank, J.E. Merz, R.G. Titus, S.M. Sogard, and M. Mangel. 2009. Steelhead life history on California's central coast: insights from a state-dependent model. Transactions of the American Fisheries Society 138:532-548.

Mangel. M., and W. H. Satterthwaite. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. Bulletin of Marine Science 83:107-130.

Collins, E.M., Titus, R.G., Beakes, M.P., Swank, D.R., Merz, J.E., Sogard, S.M., Satterthwaite, W.H., and M. Mangel. Food availability as a determinant of growth opportunity in contrasting steelhead streams in central California. In prep for Transactions of the American Fisheries Society.

Sogard, S.M., Swank, D.R., Beakes, M.P., Satterthwaite, W.H., Collins, E.M., Merz, J.E., Titus, R.G., and M. Mangel. Contrasts in growth rates and life history patterns of juvenile steelhead in stream systems of California's Central Valley and central coast. In prep for Environmental Biology of Fishes.

Kern, C., Sogard, S.M., Swank, D.R., Beakes, M.P., Satterthwaite, W.H., and M. Mangel. Contrasts in the development of seawater tolerance in steelhead from California's Central Valley and central coast. In prep for Transactions of the American Fisheries Society.

Kern, C., Merz, J.E., Sogard, S.M., Beakes, M.P., Satterthwaite, W.H., and M. Mangel. Delivery of invertebrate prey during fluctuating flows in stream systems of California's Central Valley and central coast. In prep for Ecological Applications.

Satterthwaite, W.H., S.A. Hayes, J.E. Merz, S.M. Sogard, and M. Mangel. State dependent life history of *Oncorhynchus mykiss* in central California: model testing and extensions for systems with seasonally closed lagoonal estuaries. In prep for Transactions of the American Fisheries Society.

Technical reports:

Simon, C., Satterthwaite, W.H., Beakes, M.P., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., and M. Mangel. Individual and population level variation in growth parameters for steelhead trout *Oncorhynchus mykiss* in central California. Baskin School of Engineering Technical Report UCSC-SOE-10-31.

Presentations (only the presenting author listed):

Satterthwaite, W. H. Predicting smolting and maturation of steelhead (*O. mykiss*) in central and coastal California. Poster presentation at the William R. and Lenore Mote International Symposium in Fisheries Ecology, Sarasota, FL, November 2006.

Beakes, M. Smoltification decision windows in tow California populations of steelhead: Effects of temporal variability in growth. Poster presentation at the American Fisheries Society 137th Annual Meeting, San Francisco, CA. September 2007.

Collins, Erin. Comparative Feeding and Drift Ecology of Juvenile Steelhead in Central California. Poster presentation at the American Fisheries Society 137th Annual Meeting, San Francisco, CA. September 2007.

Satterthwaite, W. H. Predicting growth and foraging in juvenile steelhead. Poster presentation at the American Fisheries Society Annual Meeting, San Francisco, CA, September 2007.

Swank, David R. Growth trajectories of wild California steelhead parr. Poster presentation at the American Fisheries Society 137th Annual Meeting, San Francisco, CA. September 2007.

Satterthwaite, W. H. Steelhead trout life history: SDP/DSV models meet data. Oral presentation at the Pacific Coast Steelhead Management Meeting, Boise, ID, March 2008.

Swank, David R. Growth trajectories of wild California steelhead parr. Oral presentation at the Pacific Coast Steelhead Management meeting, Boise, ID, March 2008.

Beakes, M.P. Smolt transformation and decision windows in two California populations of steelhead: effects of temporal variability in growth. Oral presentation at the CALFED Science Conference, Sacramento, CA, October 2008.

Collins, Erin. Comparative Feeding and Drift Ecology of Juvenile Steelhead in Central California. Oral presentation at the CalFed 5th Biennial Conference, Sacramento, CA, October 2008.

Satterthwaite, W. H. Insights from a state dependent model of steelhead life history. Oral presentation at the CALFED Science Conference, Sacramento, CA, October 2008.

Sogard, Susan M. Should I stay or should I go – life history decisions in juvenile steelhead from California's Central Valley and central coast. Invited oral presentation at the 8th International Workshop on Smoltification, Corvallis, OR, September 2009.

Sogard, Susan M. Life history decisions in steelhead: the role of growth opportunity. Oral presentation at the Salmonid Restoration Federation Conference, Santa Cruz, CA, March 2009.

Mangel, M. Tools for large scale (ecosystem-based) and long-term (evolutionary) environmental risk assessment in the marine environment. Invited oral presentation at the Okeanus Workshop on Assessing the Cumulative Impacts of Anthropogenic Stressors on Marine Mammals: From Ideas to Action, Asilomar, Pebble Beach, CA, August 2009.

Satterthwaite, W. H. Using dynamic state variable models to predict steelhead life history in four California watersheds. Invited oral presentation at the Ecological Society of America Annual Meeting, Albuquerque, NM, August 2009.

Collins, Erin. Life Histories of Central Valley Steelhead: how does the American River stock fit with the rest of the Sacramento Basin? Oral presentation at the Pacific Coast Steelhead Management Meeting, Redmond, OR, March 2010.

Collins, Erin. Life Histories of Central Valley Steelhead: how does the American River stock fit with the rest of the Sacramento Basin? Oral presentation at the Electronic Tagging Studies of Salmon Migration Symposium, Bodega Bay, CA, May 2010.

Satterthwaite, W. H. State dependent life history models of California steelhead. Invited oral presentation for the NCEAS working group on salmon, climate, and plasticity, project 12202, Seattle, WA, October 2010.

Mangel, M. Combining Life History Theory, Experiments, and Field Studies in Setting River Flow for California Steelhead. Invited oral presentation for the Lamberson Ecology Trust Lecture, Humboldt State University, in February 2010; also an invited oral presentation at the School of Fisheries and Aquatic Sciences, University of Washington, May 2010; and at Michigan State University, October 2010

Computer code: The code for all of the life history models is available at http://users.soe.ucsc.edu/~msmangel/art_bookchap1.html

Awards: The paper 'Steelhead Life History on California's Central Coast: Insights from a State-Dependent Model', with authors W.H. Satterthwaite, M.P. Beakes, E.M. Collins, D.R. Swank, J.E. Merz, R.G. Titus, S.M. Sogard, and M. Mangel, was selected as best publication for 2009 in the journal Transactions of the American Fisheries Society.

PERSONNEL THROUGHOUT THE PROJECT:

February 2006 – December 2008:

Principal Investigators: Marc Mangel, UCSC, Susan Sogard (NMFS), Rob Titus (CDG)

Post-doctoral researchers: Will Satterthwaite and Dave Swank

Technicians (full time): Erin Collins and Michael Beakes

Graduate students: Anand Patil and Chris Simon

December 2008 – July 2008: Stop work order in place, all post-docs, technicians and students were laid off

July 2008 to November 2010:

Principal Investigators: Marc Mangel, (UCSC), Susan Sogard (NMFS), and Rob Titus (CDG)

Post-doctoral researchers: Will Satterthwaite and Cynthia Kern

Technicians (part time): Noah Parker, Neosha Kashef, and David Stafford

Graduate students: Valerie Brown (UCSC)

CONTRACT MODIFICATIONS: None

NOTES/OTHER: None