Life History Variation In Steelhead Trout And The Implications For Water Mangement

prepared by Mangel, Marc Steven

submitted to Science Program 2004

compiled 2005−01−06 12:02:18 PST

Project

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The submission deadline is 2005−01−06 17:00:00 PST (approximately 5.0 hours from now).

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Instructions

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Proposal Title	***Life History Variation in Steelhead Trout and the Implications for Water Mangement***	
Institutions	University of California Santa Cruz National Marine Fisheries Service Santa Cruz Laboratory California Department of Fish and Game	*List each institution involved, one per line.*
Proposal Document		*You have already uploaded a proposal document. View it to verify that it appears as you expect. You may replace it by uploading another document*
Project Duration	***36 months***	

Is the start date a determining factor to the successful outcome of the proposed effort?
− No.
X Yes. Anticipated start date of this effort: ***2006−01−01***

Select all of the following study topics which apply to this proposal.
X life cycle models and population biology of key species
X environmental influences on key species and ecosystems
X relative stresses on key fish species
X direct and indirect effects of diversions on at−risk species
− processes controlling Delta water quality
− implications of future change on regional hydrology, water operations, and environmental processes
X water management models for prediction, optimization, and strategic assessments
− assessment and monitoring
X salmonid−related projects
− Delta smelt−related projects

Select as many keywords as necessary to describe this proposal (minimum of 3).
X adaptive management
− aquatic plants
− benthic invertebrates
X biological indicators
− birds
− neotropical migratory birds
− shorebirds
− upland birds
− wading birds
− waterfowl
− climate
− climate change
− precipitation
− sea level rise
− snowmelt
− contaminants / toxicants / pollutants
− contaminants and toxicity of unknown origin
− emerging contaminants

− mercury
− nutrients and oxygen depleting substances
− organic carbon and disinfection byproduct precursors
− persistent organic contaminants
− pesticides
− salinity
− sediment and turbidity
− selenium
− trace metals
− ***database management***
− ***economics***
− ***engineering***
− civil
− environmental
− hydraulic
− ***environmental education***
− ***environmental impact analysis***
− ***environmental laws and regulations***
− ***environmental risk assessment***
X fish biology
− bass and other centarchids
− delta smelt
− longfin smelt
− other species
X salmon and steelhead
− splittail
− striped bass
− sturgeon
X fish management and facilities
X hatcheries
− ladders and passage
− screens
− ***forestry***
− ***genetics***
− ***geochemistry***
− ***geographic information systems (GIS)***
− ***geology***
− ***geomorphology***
− ***groundwater***
X habitat
− benthos
− channels and sloughs
− flooded islands
− floodplains and bypasses
− oceanic
− reservoirs
− riparian
− rivers and streams
− shallow water
− upland habitat
− vernal pools
− water column
− wetlands, freshwater
− wetlands, seasonal
− wetlands, tidal
− ***human health***
− ***hydrodynamics***
− ***hydrology***
− ***insects***
− ***invasive species / non−native species / exotic species***
− ***land use management, planning, and zoning***
− ***limnology***
− ***mammals***
− large
− small

− ***microbiology / bacteriology***
X modeling
X conceptual
X quantitative
− ***monitoring***
X natural resource management
− ***performance measures***
− ***phytoplankton***
− ***plants***
− ***primary productivity***
− ***reptiles***
X restoration ecology
− ***riparian ecology***
− ***sediment***
− ***soil science***
− ***statistics***
− ***subsidence***
− ***trophic dynamics and food webs***
X water operations
− barriers
X diversions / pumps / intakes / exports
− gates
− levees
− reservoirs
X water quality management
− ag runoff
− mine waste assessment and remediation
− remediation
X temperature
− urban runoff
− water quality assessment and monitoring
− ***water resource management***
X water supply
− demand
− environmental water account
X water level
− water storage
X watershed management
− ***weed science***
X wildlife
X ecology
− management
− wildlife−friendly agriculture
X zooplankton
− ***administrative***

Indicate whether your project area is local, regional, or system−wide. If it is local, provide a central ZIP Code. If it is regional, provide the central ZIP Code and choose the counties affected. If it is system−wide, describe the area using information such as water bodies, river miles, and road intersections.	
− local	ZIP Code:
X regional	ZIP Code: ***95064*** counties: ***Yolo***
− system−wide	

Does your project fall on or adjacent to tribal lands?

No.

(Refer to California Indian reservations to locate tribal lands.)
If it does, list the tribal lands.

Has a proposal for this effort or a similar effort ever been submitted to CALFED for funding or to any other public agency for funding?
No.

If yes, complete the table below.

Status	Proposal Title	Funding Source	Amount	Comments

Has the lead scientist or principal investigator of this effort ever submitted a proposal to CALFED for funding or to any other public agency for funding?
No.

If yes, provide the name of the project, when it was submitted, and to which agency and funding mechanism if was submitted. Also describe the outcome and any other pertinent details describing the proposal's current status.

None to CALFED but numerous grants from NSF, NOAA, ONR over a 25 year career in UC.

All applicants must identify all sources of funding other than the funds requested through this solicitation to support the effort outlined in their proposal. Applicants must include the status of these commitments (tentative, approved, received), the source, and any cost−sharing requirements. Successful proposals that demonstrate multiple sources of funding must have the commitment of the non−Science Program PSP related funding within 30 days of notification of approval of Science Program PSP funds. If an applicant fails to secure the non−Science Program PSP funds identified in the proposal, and as a result has insufficient funds to complete the project, CBDA retains the option to amend or terminate the award. The California Bay−Delta Authority reserves the right to audit grantees.

Status	Proposal Title	Funding Source	Period Of Commitment	Requirements And Comments

Are you specifically seeking non−federal cost−share funds for this proposal?
No.

In addition to the general funds available, are you targeting additional funds set aside specifically for collaborative proposals?
No.

List people you feel are qualified to act as scientific reviewers for this proposal and are not associated with CALFED.

Full Name	Organization	Telephone	E−Mail	Expertise

Executive Summary

Provide a brief but complete summary description of the proposed project; its geographic location; project objective; approach to implement the proposal; hypotheses being tested; expected outcomes; and relationship to Science Program priorities. The Executive Summary should be a concise, informative, stand−alone description of the proposed project. *(This information will be made public on our website shortly after the closing date of this PSP.)*

Plasticity and adaptation in life histories allow populations to persist in fluctuating environments. Steelhead exhibit a remarkable range of life histories, yet continue to decline in abundance throughout California. The research proposed here will examine (through models, laboratory experiments, and field work) the hypothesis that alteration of the amount of water flow and the temporal pattern of its delivery in a watershed impact the life history trajectory selected by juvenile steelhead. Alteration of the complex linkage between life history strategies and survival potentially contributes to the continuing decline of steelhead populations. The mechanism underlying a particular trajectory is presumed to be an interacting function of growth rates, body condition, and the temporal pattern of changes in these attributes during the first year of life. Growth opportunity is likely to be greatly modified by changes in water flow, primarily through accompanying changes in temperature, available habitat, and food delivery in the form of drifting invertebrates. We will use a three−pronged approach of laboratory, field, and modeling studies to investigate the environmental factors that determine life history transitions and pathways for age−0 steelhead, how these patterns vary across different populations and watersheds, how modification in flow regimes impacts growth opportunity and subsequent life history decisions, and how these life history transitions affect population dynamics. Laboratory experiments will examine the timing of decision windows that set an individual on one of three pathways: emigration at age−1, continued residence in freshwater prior to emigration, or early maturation. Central Valley and central California coast populations will be used to assess population differences in growth responses and selected trajectories. Field studies will focus on the seasonal variability in environmental factors for age−0 steelhead in four watersheds, two in the Central Valley and two on the central California coast. Physical parameters of temperature and flow rates, and biological parameters of food availability and competitor density will be monitored throughout a three year time period. Growth rates will be measured in tagged fish to evaluate correspondence with expectations based on environmental factors. Data from lab and field studies will be incorporated into life cycle and population models of California steelhead. Results of all three approaches will be used to develop predictive models of life history consequences under varying environmental conditions and water policy decisions. These scenarios will be valuable in assessing the implications of different water management regimes for continued persistence of steelhead populations in freshwater ecosystems of the Central Valley and other California regions. . Our work will thus focus on CalFed priority topic areas of ecological processes and their relationship to water management and key species and water operations and biological resources. Furthermore, our work will provide tools and data to help achieve the CVPIA Section 3406(b)1 objective of doubling populations of naturally produced salmonids.

Give additional comments, information, etc. here.

Applicant

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All information on this page is to be provided for the agency or institution to whom funds for this proposal would be awarded.

Applicant Institution	***University of California Santa Cruz***	*This list comes from the project form.*
Applicant Institution Type	***public institution of higher education***	

Institution Contact

Please provide information for the primary person responsible for oversight of grant operation, management, and reporting requirements.

Salutation	***Professor***
First Name	***Marc***
Last Name	***Mangel***
Street Address	***AMS, UC Santa Cruz***
City	***Santa Cruz***
State Or Province	***CA***
ZIP Code Or Mailing Code	***95064***
Telephone	***8312342970*** *Include area code.*
E−Mail	***msmangel@ucsc.edu***

Additional information regarding prior applications submitted to CALFED by the applicant organization or agency and/or funds received from CALFED programs by applicant organization or agency may be required.

Personnel

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Instructions

Applicants must provide brief biographical sketches, titles, affiliations, and descriptions of roles, relevant to this effort, of the principal and supporting project participants by completing a Personnel Form. This includes the use of any consultants, subcontractors and/or vendors; provide information on this form for all such people.

Information provided on this form will automatically support subsequent forms to be completed as part of the Science PSP submission process. Please be mindful of what information you enter and how it may be represented in the Task and Budget forms.

Information regarding anticipated subcontractor services must be provided regardless if the specific service provider has been selected or not. If the specific subcontractor has not been identified or selected, please list TBD (to be determined) in the Full Name field and the anticipated service type in the Title field (example: Hydrology Expert).

Please provide this information before continuing to those forms.

Mangel, Marc, Ph.D.

*This person is the **Lead Investigator**. Contact information for this person is required.*

Full Name	***Mangel, Marc, Ph.D.***	example: Wright, Jeffrey R., PhD.
Institution	***University of California Santa Cruz***	*This list comes from the project form.*
Title	***Professor of Applied Mathematics and Statistics, Director Center for Stock Assessment Research***	*example: Dean of Engineering*
Position Classification	***primary staff***	
Responsibilities	Lead on the modeling, on connecting models with data, and on management implications	
Qualifications		*You have already uploaded a PDF file for this question. Review the file to verify that appears correctly.*
Mailing Address	***AMS, UC Santa Cruz***	
City	***Santa Cruz***	
State	***CA***	
ZIP	***95064***	
Business Phone	***8314595797***	
Mobile Phone	***8312342970***	
E−Mail	***msmangel@ucsc.edu***	

Describe other staff below. If you run out of spaces, submit your updates and return to this form.

Sogard, Susan, Ph.D.

Full Name	***Sogard, Susan, Ph.D.***	example: Wright, Jeffrey R., PhD. Leave blank if name not known.
Institution	***National Marine Fisheries Service Santa Cruz Laboratory***	*This list comes from the project form.*

Title	***Supervisory Research Fishery Biologist, NMFS Santa Cruz Laboratory (NMFS/SCL)***	*example: Dean of Engineering*
Position Classification	***primary staff***	
Responsibilities	Field and laboratory experiment conceptualization and execution	
Qualifications		***This is only required for primary staff.*** *You have already uploaded a PDF file for this question. Review the file to verify that appears correctly.*

Titus, Robert G., Ph.D.

Full Name	***Titus, Robert G., Ph.D.***	example: Wright, Jeffrey R., PhD. Leave blank if name not known.
Institution		*This list comes from the project form.*
Title	***Senior Environmental Scientist (senior supervisor), California Department of Fish and Game (CDFG)***	*example: Dean of Engineering*
Position Classification	***primary staff***	
Responsibilities	Field study conceptualization and execution	
Qualifications		***This is only required for primary staff.*** *You have already uploaded a PDF file for this question. Review the file to verify that appears correctly.*

Postdoctoral Researcher 1

Full Name		example: Wright, Jeffrey R., PhD. Leave blank if name not known.
Institution	***University of California Santa Cruz***	*This list comes from the project form.*
Title	***Postdoctoral researcher 1***	*example: Dean of Engineering*
Position Classification	***secondary staff***	
Responsibilities	Work with Marc Mangel on developing the models	
Qualifications		***This is only required for primary staff.*** *Upload a PDF version of this person's resume that is no more than five pages long. To upload a resume, use the "Browse" button to select the PDF file containing the resume.*

Postdoctoral Researcher 2

Full Name		example: Wright, Jeffrey R., PhD. Leave blank if name not known.
Institution	***National Marine Fisheries Service Santa Cruz Laboratory***	*This list comes from the project form.*
Title	***Postdoctoral researcher 2***	*example: Dean of Engineering*
Position Classification	***secondary staff***	
Responsibilities	Work with Susan Sogard and Robert Titus on laboratory and field experiments	
Qualifications		***This is only required for primary staff.***

		Upload a PDF version of this person's resume that is no more than five pages long. To upload a resume, use the "Browse" button to select the PDF file containing the resume.

Postgraduate Research Assistant

Full Name		example: Wright, Jeffrey R., PhD. Leave blank if name not known.
Institution	***University of California Santa Cruz***	*This list comes from the project form.*
Title	***Postgraduate Research Assistant***	*example: Dean of Engineering*
Position Classification	***secondary staff***	
Responsibilities	Work with Marc Mangel and PD1 on data collection, organization and assmilation	
Qualifications		***This is only required for primary staff.*** *Upload a PDF version of this person's resume that is no more than five pages long. To upload a resume, use the "Browse" button to select the PDF file containing the resume.*

Laboratory Assistant

Full Name		example: Wright, Jeffrey R., PhD. Leave blank if name not known.
Institution	***National Marine Fisheries Service Santa Cruz Laboratory***	*This list comes from the project form.*
Title	***Laboratory Assistant***	*example: Dean of Engineering*
Position Classification	***secondary staff***	
Responsibilities	Work with Susan Sogard and Robert Titus on field and experimental studies	
Qualifications		***This is only required for primary staff.*** *Upload a PDF version of this person's resume that is no more than five pages long. To upload a resume, use the "Browse" button to select the PDF file containing the resume.*

Technician

Full Name		example: Wright, Jeffrey R., PhD. Leave blank if name not known.
Institution	***University of California Santa Cruz***	*This list comes from the project form.*
Title	***Technician***	*example: Dean of Engineering*
Position Classification	***secondary staff***	
Responsibilities	Work with Robert Titus on field sampling and detailed analysis of field samples	
Qualifications		***This is only required for primary staff.*** *Upload a PDF version of this person's resume that is no more than five pages long. To upload a resume, use the "Browse" button to select the PDF file containing the resume.*

Conflict Of Interest

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Instructions

To help Science Program staff manage potential conflicts of interest in the review and selection process, we need some information about who will directly benefit if your proposal is funded. We need to know of individuals in the following categories:

- Applicants listed in the proposal who wrote the proposal, will be performing the tasks listed in the proposal, or who will benefit financially if the proposal is funded;
- Subcontractors listed in the proposal who will perform some tasks listed in the proposal and will benefit financially if the proposal is funded.

Applicant	University of California Santa Cruz
Submittor	Mangel, Marc Steven
Primary Staff	Mangel, Marc, Ph.D.
Primary Staff	Sogard, Susan, Ph.D.
Primary Staff	Titus, Robert G., Ph.D.
Secondary Staff	*Postdoctoral researcher 1
Secondary Staff	*Postdoctoral researcher 2
Secondary Staff	*Postgraduate Research Assistant
Secondary Staff	*Laboratory Assistant
Secondary Staff	*Technician

Are there other persons not listed above who helped with proposal development?
No.

If there are, provide below the list of names and organizations of all individuals not listed in the proposal who helped with proposal development along with any comments.

Tasks

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Instructions

Utilize this Task Table to delineate the tasks identified in your project description. Each task and subtask must have a number, title, brief description of the task (detailed information should be provided in the project description), timeline, list of personnel or subcontractors providing services on each specific task, and list of anticipated deliverables (where appropriate). When creating subtasks, information must be provided in a way that avoids duel presentation of supporting tasks within the overall task (i.e. avoid double counting). Information provided in the Task Table will be used to support the Budget Form. Ensuring information regarding deliverables, personnel and costs associated with subtasks are only provided once is imperative for purposes of avoiding double counting of efforts within the Budget Form.

For proposals involving multiple institutions (including subcontractors), the table must clearly state which institutions are performing which tasks and subtasks.

Task ID	Task Name	Start Month	End Month	Personnel Involved	Description	Deliverables
1	*Extend Theory of Thorpe et al*	*1*	*24*	*Mangel, Marc, Ph.D. *Postdoctoral researcher 1 *Postgraduate Research Assistant*	Mangel and Post−doc, in consultation with Sogard and Titus will extend the theory of Thorpe et al to account for steelhead in California and will parametrize the models with data collected during the empirical work	Computer models, peer−reviewed journal articles, final report to CalFED, presentations at CalFed and other scientific meetings
2	*Test the theory*	*25*	*36*	*Mangel, Marc, Ph.D. *Postdoctoral researcher 1 *Postgraduate Research Assistant*	The theory developed in Task 1 will be tested through experimental and observational studies (Tasks 3−8_	Data analyses, development of a database with field and experimental data, peer−reviewed journal articles, final report to CalFED, presentations at CalFed and other scientific meetings
3	*Laboratory Growth Experiment 1*	*5*	*17*	*Sogard, Susan, Ph.D. *Postdoctoral researcher 2 *Laboratory Assistant*	Conduct lab experiments designed to determine the influence of growth patterns on emigration at age 1 in juvenile steelhead. Factors include two populations (Scott Creek and Battle Creek) and four ration treatments, with fish held at restricted levels except for a varying two month period of unlimited food availability. Photoperiod will match the natural cycle of a latitude mid−way between the two population locations, and temperatures will be moderate, matching those experienced on average by the Scott Creek population. Measured variables will include monthly growth rates in length and weight, behavioral assays of activity and aggression in mid−winter, Na+K+ATPase levels in April, and responses to seawater challenges in April.	Final report to CalFed, presentations at CalFed and other scientific meetings, publication in peer−reviewed scientific journal
4	*Laborator Growth Experiment 2*	*17*	*29*	*Sogard, Susan, Ph.D. *Postdoctoral researcher 2 *Laboratory Assistant*	: Conduct lab experiments designed to determine the influence of growth patterns on emigration at age 1 in juvenile steelhead. Factors include two populations (Scott Creek and Battle Creek) and four ration treatments, with fish held at restricted levels except for a varying two month period of unlimited food availability. Photoperiod will match the natural cycle of a latitude mid−way between the two population locations, and temperatures will be moderate, matching those experienced on average by the Battle Creek population. Measured variables will include monthly	Final report to CalFed, presentations at CalFed and other scientific meetings, publication in peer−reviewed scientific journal

					growth rates in length and weight, behavioral assays of activity and aggression in mid−winter, Na+K+ATPase levels in April, and responses to seawater challenges in April.	
5	***Laboratory Maturation Experiment***	***29***	***36***	***Sogard, Susan, Ph.D. *Postdoctoral researcher 2 *Laboratory Assistant***	Conduct laboratory experiments to define the timing of the maturation decision window. Factors include two populations and four ration treatments with variable timing of a switch to restricted rations. Measured variables include monthly length and weight and gender and maturation status in April.	Final report to CalFed, presentations at CalFed and other scientific meetings, publication in peer−reviewed scientific journal
6	***Field estimates of juvenile steehead densities***	***1***	***36***	***Sogard, Susan, Ph.D. Titus, Robert G., Ph.D. *Postdoctoral researcher 2 *Postgraduate Research Assistant *Technician***	Estimate seasonal densities of juvenile steelhead in two central California coast creeks and two Central Valley rivers using snorkeling techniques supplemented by electro−shock fishing and seining	Final report to CalFed, presentations at CalFed and other scientific meetings, publication in peer−reviewed scientific journal
7	***Field estimates of invertebrate prey densities***	***1***	***36***	***Sogard, Susan, Ph.D. Titus, Robert G., Ph.D. *Postdoctoral researcher 2 *Laboratory Assistant *Technician***	Estimate seasonal patterns in food availability at four sites in each of four streams using standard benthic and drift sampling techniques. Sampling will occur over four time periods per year in each of three years, with one 48 hour sampling series for each of the 16 sites during the 3 year period.	Final report to CalFed, presentations at CalFed and other scientific meetings, publication in peer−reviewed scientific journal
8	***Natural growth variability in juvenile steelhead***	***1***	***36***	***Sogard, Susan, Ph.D. Titus, Robert G., Ph.D. *Postdoctoral researcher 2 *Laboratory Assistant *Technician***	Estimate natural growth rates of juvenile steelhead in four stream systems, using mark and recapture techniques in each of 3 years. Fish < 65 mm will be tagged with elastomer and fish > 65 mm will be tagged with PIT tags. Recaptures will be conducted in association with seining and electro−shock fishing efforts	Final report to CalFed, presentations at CalFed and other scientific meetings, publication in peer−reviewed scientific journal

Budget

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Instructions

All applicants must complete a budget for each task and subtask. The Budget Form uses data entered in the Task Form, thus tasks should be entered before starting this form. Failure to complete a Budget Form for each task and/or subtask will result in removal of the application from consideration for funding.

CBDA retains the right to request additional information pertaining to the items, rates, and justification of the information presented in the Budget Form(s).

Supporting details on how costs were derived for each line item must be included in the justification section for each item. The cost detail for each item should include the individual cost calculations associated with each line item to provide the basis for determining the total amount for each budget category.

Following are guidelines for completing the justification section of this form:

Labor (Salary &Wages)

Ensure each employee and associated classification is correctly identified for each task and subtask. This information will automatically be provided once the Staff Form has been completed. Provide estimated hours and hourly rate of compensation for each position proposed in the project.

Employee Benefits

Benefits, calculated as a percentage of salaries, are contributions made by the applicant for sick leave, retirement, insurance, etc. Provide the overall benefit rate and specify benefits included in this rate for each employee classification proposed in the project.

Travel

Travel includes the cost of transportation, subsistence, and other associated costs incurred by personnel during the term of the project. Provide purpose and estimated costs for all travel. Reoccurring travel costs for a particular task or subtask may be combined into one entry. The number of trips and cost for each occurrence must be clearly represented in the justification section for reoccurring travel items of this nature.

Any reimbursement for necessary travel and per diem shall be at rates specified by the California Department of Personnel Administration for similar employees (www.dpa.ca.gov/jobinfo/statetravel.shtm).

Equipment

Equipment is classified as any item of $5,000 or more and has an expected life of three years or more. Equipment purchased in whole or in part with these grant funds must be itemized. List each piece of equipment and provide a brief description and justification for each.

Supplies

Provide a basic description and cost for expendable research supplies. Costs associated with GIS services, air photos, reports, etc. must be listed separately and have a clear justification associated with each entry. Postage, copying, phone, fax and other basic operational costs associated with each task and subtask may be combined unless the cost associated with one particular service is unusually excessive.

Subcontractor Services

Subcontractor services (Professional and Consultant services) include the total costs for any services needed by the applicant to complete the project tasks. Ensure the correct organization is entered in the Personnel Form so that it appropriately appears on the Budget Form. The applicant must provide all associated costs of all subcontractors (i.e. outside service providers) when completing this form. Applicants must be able to demonstrate that all subcontractors were selected according to an applicant's institutional requirements for the selection of subcontractors (competitive selection or sole source justification).

CBDA retains the right to request that a subcontractor provide cost estimates in writing prior to distribution of grant funds.

CBDA retains the right to request consultant, subcontractor, and/or outside service provider cost estimates in writing prior to distribution of grant funds.

Indirect Costs (Overhead)

Indirect costs are overhead expenses incurred by the applicant organization as a result of the project but are not easily identifiable with a specific project. The indirect cost rate consists of a reasonable percentage of all costs to run the agency or organization while completing the project. List the cost and items associated with indirect costs. (These items may include general office expenses such as rent, office equipment, administrative staff, operational costs, etc. Generally these items are represented by the applicant through a predetermined percentage or surcharge separate from other specific costs of items necessary to complete a specific task or subtask.)

If indirect cost rates are different for State and Federal funds, please identify each rate and the specific items included in the calculation for that rate.

Task 1, Extend Theory Of Thorpe Et Al: Labor	**Justification**	**Amount**
Mangel, Marc, Ph.D.	***Mangel will spend one summer month and 15% of the academic year developing the theory***	***75006***
***Postdoctoral Researcher 1**	***100% time developing the theory, fitting models to data, assisting in field studies when needed***	***92087***
***Postgraduate Research Assistant**	***Library work, organizing data, and the simpler analyses; assisting in field studies when needed***	***16895***
Task 1, Extend Theory Of Thorpe Et Al: Benefits	**Justification**	**Amount**
Mangel, Marc, Ph.D.	***13.5% summer, 15% academic year***	***11633***
***Postdoctoral Researcher 1**	***25% calendar year***	***21218***
***Postgraduate Research Assistant**	***22% calendar year***	***3717***
Task 1, Extend Theory Of Thorpe Et Al: Travel Expenses	**Justification**	**Amount**
Conferences	***Present work***	***3000***
Task 1, Extend Theory Of Thorpe Et Al: Supplies And Expendables	**Justification**	**Amount**
Other	***As required for project (software, phone, fax, paper)***	***3000***
Task 1, Extend Theory Of Thorpe Et Al: Subcontractors	**Justification**	**Amount**
No subcontractor was assigned to this task.		
Task 1, Extend Theory Of Thorpe Et Al: Equipment	**Justification**	**Amount**
Computers (2)	***Top of the line desktop machines needed for this work`***	***11000***
Task 1, Extend Theory Of Thorpe Et Al: Other Direct	**Justification**	**Amount**
Maintenance Fees	***Required for all equipment at UCSC***	***30000***
Task 1, Extend Theory Of Thorpe Et Al: Indirect (Overhead)	**Justification**	**Amount**
Indirect Costs UCSC	***49% rate***	***102682***
	Task 1 Total	$370,238
Task 2, Test The Theory: Labor	**Justification**	**Amount**
Mangel, Marc, Ph.D.	***As in task 1***	***39780***
***Postdoctoral Researcher 1**	***As in task 1***	***47800***
***Postgraduate Research Assistant**	***As in task 1***	***8415***
Task 2, Test The Theory: Benefits	**Justification**	**Amount**
Mangel, Marc, Ph.D.	***As in task 1***	***6660***
***Postdoctoral Researcher 1**	***As in task 1***	***11950***
***Postgraduate Research Assistant**	***As in task 1***	***1851***
Task 2, Test The Theory: Travel Expenses	**Justification**	**Amount**
Conferences	***As in task 1***	***1500***
Task 2, Test The Theory: Supplies And Expendables	**Justification**	**Amount**
Other	***As in task 1***	***1500***
Task 2, Test The Theory: Subcontractors	**Justification**	**Amount**
No subcontractor was assigned to this task.		
Task 2, Test The Theory: Equipment	**Justification**	**Amount**
Task 2, Test The Theory: Other Direct	**Justification**	**Amount**
Maintenance Fees	***As in task***	***1378***

Task 2, Test The Theory: Indirect (Overhead)	**Justification**	**Amount**
Indirect Costs At UCSC	***49%***	***59207***
	Task 2 Total	$180,041
Task 3, Laboratory Growth Experiment 1: Labor	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***100% salary paid by NMFS***	***0***
***Postdoctoral Researcher 2**	***100% calendar year on the details of laboratory and field work***	***22500***
***Laboratory Assistant**	***100% calendar year on the details of laboratory and field project***	***17500***
Task 3, Laboratory Growth Experiment 1: Benefits	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***Paid by NMFS***	***0***
***Postdoctoral Researcher 2**	***25%***	***5625***
***Laboratory Assistant**	***25%***	***4375***
Task 3, Laboratory Growth Experiment 1: Travel Expenses	**Justification**	**Amount**
		0
Task 3, Laboratory Growth Experiment 1: Supplies And Expendables	**Justification**	**Amount**
Other	***Tanks, plumbing, fish good, enzyme kits***	***5000***
Task 3, Laboratory Growth Experiment 1: Subcontractors	**Justification**	**Amount**
No subcontractor was assigned to this task.		
Task 3, Laboratory Growth Experiment 1: Equipment	**Justification**	**Amount**
One Aquarium Chiller Unit	***Needed to maintain fish in the laboratory***	***5000***
Task 3, Laboratory Growth Experiment 1: Other Direct	**Justification**	**Amount**
Task 3, Laboratory Growth Experiment 1: Indirect (Overhead)	**Justification**	**Amount**
UCSC/NMFS Partnership Costs	***26.4%***	***15810***
	Task 3 Total	$75,810
Task 4, Laborator Growth Experiment 2: Labor	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***As in task 3***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***23175***
***Laboratory Assistant**	***As in task 3***	***18025***
Task 4, Laborator Growth Experiment 2: Benefits	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***As in task 3***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***5794***
***Laboratory Assistant**	***As in task 3***	***4506***
Task 4, Laborator Growth Experiment 2: Travel Expenses	**Justification**	**Amount**
Task 4, Laborator Growth Experiment 2: Supplies And Expendables	**Justification**	**Amount**
Other	***Plumbing, fish food, videotapes, videosoftwre, enzyme kits***	***2000***
Task 4, Laborator Growth Experiment 2: Subcontractors	**Justification**	**Amount**
No subcontractor was assigned to this task.		
Task 4, Laborator Growth Experiment 2: Equipment	**Justification**	**Amount**
Task 4, Laborator Growth Experiment 2: Other Direct	**Justification**	**Amount**
Task 4, Laborator Growth Experiment 2: Indirect (Overhead)	**Justification**	**Amount**
UCSC/NMFS Partnership	***As in task 3***	***15869***
	Task 4 Total	$69,369
Task 5, Laboratory Maturation Experiment: Labor	**Justification**	**Amount**

Sogard, Susan, Ph.D.	***As in task 3***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***23870***
***Laboratory Assistant**	***As in task 3***	***18565***
Task 5, Laboratory Maturation Experiment: Benefits	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***As in task 3***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***5968***
***Laboratory Assistant**	***As in task 3***	***4642***
Task 5, Laboratory Maturation Experiment: Travel Expenses	**Justification**	**Amount**
Task 5, Laboratory Maturation Experiment: Supplies And Expendables	**Justification**	**Amount**
Other	***Plumkbing, fish food, videotapes, enzyme kits***	***2000***
Task 5, Laboratory Maturation Experiment: Subcontractors	**Justification**	**Amount**
No subcontractor was assigned to this task.		
Task 5, Laboratory Maturation Experiment: Equipment	**Justification**	**Amount**
Task 5, Laboratory Maturation Experiment: Other Direct	**Justification**	**Amount**
Task 5, Laboratory Maturation Experiment: Indirect (Overhead)	**Justification**	**Amount**
UCSC/NMFS Partnership	***As in task 3***	***16342***
	Task 5 Total	$71,387
Task 6, Field Estimates Of Juvenile Steehead Densities: Labor	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***As in task 3***	***0***
Titus, Robert G., Ph.D.	***100% salary paid by CDFG***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***23182***
***Postgraduate Research Assistant**		
***Technician**	***Needed for field sampling and analysis***	***32000***
Task 6, Field Estimates Of Juvenile Steehead Densities: Benefits	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***As in task 3***	***0***
Titus, Robert G., Ph.D.	***100% paid by CDFG***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***5796***
***Postgraduate Research Assistant**		
***Technician**	***25%***	***8000***
Task 6, Field Estimates Of Juvenile Steehead Densities: Travel Expenses	**Justification**	**Amount**
Other	***8 trips to field sites***	***4000***
Task 6, Field Estimates Of Juvenile Steehead Densities: Supplies And Expendables	**Justification**	**Amount**
Other	***Temperature recorders, flow meters, snorkeling gear, data recording supplies***	***8000***
Task 6, Field Estimates Of Juvenile Steehead Densities: Subcontractors	**Justification**	**Amount**
No subcontractor was assigned to this task.		
Task 6, Field Estimates Of Juvenile Steehead Densities: Equipment	**Justification**	**Amount**
Task 6, Field Estimates Of Juvenile Steehead Densities: Other Direct	**Justification**	**Amount**
Task 6, Field Estimates Of Juvenile Steehead Densities: Indirect	**Justification**	**Amount**

(Overhead)		
UCSC/NMFS Partnership	***As in task 3***	***26374***
	Task 6 Total	$107,352
Task 7, Field Estimates Of Invertebrate Prey Densities: Labor	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***As in task 3***	***0***
Titus, Robert G., Ph.D.	***As in task 6***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***23182***
***Laboratory Assistant**	***As in task 3***	***18030***
***Technician**	***As in task 6***	***32000***
Task 7, Field Estimates Of Invertebrate Prey Densities: Benefits	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***As in task 3***	***0***
Titus, Robert G., Ph.D.	***As in task 6***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***5796***
***Laboratory Assistant**	***As in task 3***	***4508***
***Technician**	***As in task***	***8000***
Task 7, Field Estimates Of Invertebrate Prey Densities: Travel Expenses	**Justification**	**Amount**
Other	***8 trips to field sties***	***4000***
Task 7, Field Estimates Of Invertebrate Prey Densities: Supplies And Expendables	**Justification**	**Amount**
Other	***Invertebrate samplers, nets, collecting gear, sample processing supplies***	***10000***
Task 7, Field Estimates Of Invertebrate Prey Densities: Subcontractors	**Justification**	**Amount**
No subcontractor was assigned to this task.		
Task 7, Field Estimates Of Invertebrate Prey Densities: Equipment	**Justification**	**Amount**
Task 7, Field Estimates Of Invertebrate Prey Densities: Other Direct	**Justification**	**Amount**
Task 7, Field Estimates Of Invertebrate Prey Densities: Indirect (Overhead)	**Justification**	**Amount**
UCSC/NMFS Partnership	***As in task 3***	***27010***
	Task 7 Total	$132,526
Task 8, Natural Growth Variability In Juvenile Steelhead: Labor	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***As in task 3***	***0***
Titus, Robert G., Ph.D.	***As in task 6***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***23182***
***Laboratory Assistant**	***As in task 3***	***18030***
***Technician**	***As in task 6***	***32000***
Task 8, Natural Growth Variability In Juvenile Steelhead: Benefits	**Justification**	**Amount**
Sogard, Susan, Ph.D.	***As in task 3***	***0***
Titus, Robert G., Ph.D.	***As in task 6***	***0***
***Postdoctoral Researcher 2**	***As in task 3***	***5796***
***Laboratory Assistant**	***As in task 3***	***4508***
***Technician**	***As in task 6***	***8000***
Task 8, Natural Growth Variability In Juvenile Steelhead: Travel Expenses	**Justification**	**Amount**

Other	*8 trips to field sites*	*4000*
Task 8, Natural Growth Variability In Juvenile Steelhead: Supplies And Expendables	**Justification**	**Amount**
Other	*PIT tags, elastomer, seines, electroshock fishing accessory gear, buckets, measuring gear*	*7000*
Task 8, Natural Growth Variability In Juvenile Steelhead: Subcontractors	**Justification**	**Amount**
No subcontractor was assigned to this task.		
Task 8, Natural Growth Variability In Juvenile Steelhead: Equipment	**Justification**	**Amount**
Task 8, Natural Growth Variability In Juvenile Steelhead: Other Direct	**Justification**	**Amount**
Task 8, Natural Growth Variability In Juvenile Steelhead: Indirect (Overhead)	**Justification**	**Amount**
UCSC/NMFS Partnership	*As in task 3*	*26856*
	Task 8 Total	$129,372
	Grand Total	$1,136,095

− The indirect costs may change by more than 10% if federal funds are awarded for this proposal.

What is the total of non−federal funds requested?

Life History Variation in Steelhead Trout and the Implications for Water Management

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Project Purpose

Steelhead (*Oncorhynchus mykiss*) exhibit a remarkable diversity of life histories. At the end of their first year, steelhead follow three possible trajectories: smolt transformation and emigration to the ocean, remaining in freshwater as immature parr, or precocious maturation. Following the first year, multiple pathways are again possible, such as emigration or continued freshwater residence. Some individuals never emigrate, thus becoming rainbow trout, the non-anadromous form of *O. mykiss*. In contrast to other Pacific salmonids, steelhead are iteroparous and may spawn over several years, returning to the ocean between each spawning. These life history pathways are presumed to be the consequence of an interaction between genetic thresholds and environmental context; i.e. the genetic program is cued by the environment. Natural and artificial selection affect the genetic framework, and water policy and other anthropogenic factors affect the environment.

This complexity of life histories makes understanding population dynamics and environmental effects on steelhead very challenging. For example, fisheries science typically focuses on analysis of annual cohorts (year classes) and how they fare as they progress through their life span. However, steelhead progeny produced in a single year will very likely split into many trajectories, inhibiting the tracking of birth cohorts. The returning run of adults will be comprised of fish of different ages that have spent varying periods in freshwater and seawater, making linkages of abundance to environmental conditions (i.e., flow rates in the birth year) problematic. An improved understanding of how individuals arrive at a particular life history pathway will greatly improve our ability to monitor and predict effects of changing environments on steelhead populations. Our work will thus focus on CalFed priority topic areas of ecological processes and their relationship to water management and key species and water operations and biological resources. Furthermore, our work will provide tools and data to help achieve the

CVPIA Section 3406(b)1 objective of doubling populations of naturally produced salmonids. Understanding the environmental conditions necessary for success of fish adopting different life history strategies is also essential for CVPIA goals of restoring altered habitats and providing water flows of appropriate timing to protect early stages of steelhead. In addition, the results will be directly applicable to understanding ongoing anadromy vs. residency issues for *O. mykiss*, such as reversals of life history types (switching across generations between anadromy and non-anadromy, Zimmerman and Reeves 2000, Thrower et al. in press), the degree of genetic relatedness and natural cross-mating, and the potential role of non-anadromous populations in contributing to restoration of the anadromous life history.

The diversity of life histories in *O. mykiss* is a bet-hedging strategy promoting persistence of populations in highly variable environments (Mangel and Clark 1988, Thorpe et al 1998). However, despite this flexibility steelhead populations continue to decline in abundance. In California, all but one Evolutionarily Significant Unit (ESU) of steelhead are currently listed as either threatened or endangered under the Endangered Species Act. In the Central Valley, declines are clearly linked to water management (McEwan 2001). Dam construction throughout the Sacramento and San Joaquin watersheds eliminated approximately 82% of historical spawning and rearing habitat (Yoshiyama et al. 1996 in McEwan 2001) and constrained steelhead to spawning in lower elevations. However, the continuing decline of steelhead populations 40+ years after the major period of dam construction suggests that other factors are contributing to population losses. McEwan (2001) suggests 1) Increasing water exports by State Water Project and Central Valley Project pumping facilities contribute to further degradation of habitat quality in the remaining spawning and rearing locations accessible to steelhead. 2) Density-dependent growth responses associated with reduced populations may increase the proportion of steelhead that residualize (never migrate to the ocean). 3) Metapopulation dynamics (Cooper and Mangel 1999) interacting with habitat loss may be contributing to continuing abundance declines. In a dynamic system such as the Central Valley, extirpation of small populations that occasionally replenish large populations or reduction of large source populations that sustain smaller sink populations may lead to overall declines in total abundance of the ESU.

In this project we will focus on determining and modeling the environmental conditions that underlie the three pathways available to steelhead in their first year. Prior studies on juvenile salmonids have demonstrated the influence of growth and lipid accumulation, interacting with genetic factors, on timing of life history transitions (i.e., Thorpe et al. 1998). Fast growth is typically associated with smolt transformation and emigration at age 1. Fish with poor growth typically remain in freshwater for at least another year. Early maturation may occur in fish that are able to both grow quickly and accumulate high levels of lipids. Once initiated, these trajectories may be fixed, with limited opportunity to switch if conditions change. However, major shifts in the environment can result in a high proportion of fish that have entered an inappropriate pathway. Our overall hypothesis is that water flow levels and the temporal pattern of water delivery have a major impact on growth opportunity and life history expression in age-0 steelhead, which will echo through the rest of their life history and population dynamics. Alteration of water flow patterns potentially disrupts the natural adaptive responses of juvenile steelhead, resulting in reduced survival as fish make crucial mistakes in selected life history trajectories. In order to reach CVPIA goals of increasing naturally produced salmonids, one must understand how the environment affects the life history processes and how those processes are echoed through to production.

We propose investigating a series of questions concerning the factors determining the timing of emigration in juvenile steelhead and the role of environment, particularly water flows, in shaping this behavior. These include:

1) How does one modify the conceptual framework of Thorpe et al. (1998), which is described below, to account for the relatively unique biogeography of California?
2) What predictions emerge from this modified framework?
3) What information do size distributions and growth rate provide about the probability of migration?
4) How do coastal steelhead differ from Central Valley steelhead in these regards? Is this evidence for local adaptation or developmental plasticity?
5) What are the implications of these results for the effects of water flows on steelhead survival and migration?

We will address these questions from approaches of field studies, lab experiments, and modeling.

Background

Life-history strategies are the means by which organisms achieve successful reproduction in varying environments. It is common to approach the study of life histories from two perspectives. With the ultimate or functional perspective the goal is measuring fitness in terms of representation in future generations. Ultimate considerations are post-hoc because they attribute fitness to individuals at the completion of the particular phase of the life cycle and do not attempt to characterize the mechanisms that animals use to achieve the optimum life history pattern. The proximate or physiological perspective focuses on the developmental pathways that are the consequences of individual responses to the opportunities offered by the environment.

Salmonid life histories are characterized by two developmental conversions: smolt metamorphosis and maturation. Atlantic salmon *Salmo salar* typically spawn in autumn and first feeding of the offspring is in the following spring (April/May). Determination of whether an individual will undergo smolt metamorphosis the following spring (at age 1) occurs soon after midsummer (Thorpe et al 1998), but this timing is not known for any other salmonids. Regarding maturation, the key observation (Policansky 1983) is that fish with access to abundant resources and stable conditions for development mature as soon as they are able to do so. Both males and females have the potential to mature at age 0+ (typically described as 'precocious' maturation), but it is more commonly expressed in males. (However, in cases of landlocked populations, both males and females mature without migration and at small size (13-15 cm); see Behnke (2002) pg 243 for an example.)

Thorpe et al. (1998, also see Mangel 1994) developed an approach to understanding the life history of Atlantic salmon that combines ultimate (evolutionary) and proximate (physiological) considerations. In this approach, fish life histories are regulated by inhibition (of smolt metamorphosis and of maturation) or the release of inhibition at certain points in the calendar year (decision windows). Whether or not inhibition is released depends on projections of physiological state into the future, based on current information (Fig. 1). This framework has been successfully applied to Atlantic salmon in both North America and Europe, and to chinook salmon *Oncorhynchus tschawytscha* in British Columbia and Washington respectively (W. Dickhoff, presentation to the Recovery Science Review Panel, 30 Aug 04, using data from Beckman et al (2003) and Larsen et al (2004)).

Experimental studies have elucidated the importance of early growth rates and the position of an individual along an expected growth trajectory in shaping the probability of early maturation and/or migration, as well as the timing of emigration for anadromous individuals, with the following general sequence for Atlantic salmon (outlined in Thorpe et al. 1998). In the spring, a maturation switch occurs in which current energetic state (lipid reserves) and the rate of change in state are compared with a genetically determined maturation threshold. Individuals exceeding the threshold adopt a pathway of early maturation. Near the end of their first summer, juveniles enter a second decision window of assessment of internal state (body size) and its rate of change (i.e. growth rate). If the threshold is exceeded, the individual adopts a migratory pathway and continues to feed and have high activity levels during the winter in preparation for smolting in the spring. If the threshold is not attained, the individual adopts a non-migratory pathway, reducing its activity and thus its vulnerability during the winter. Following this decision, the population in general will divide into two size modes as fish on the emigrating pathway continue to increase in size relative to the non-emigrating mode. Fish that have adopted the maturation pathway do not initiate the emigration process. As a consequence of these life history decisions, fast growing age-0 individuals with high lipid accumulation may mature as parr, individuals growing at moderately fast rates are likely to undergo smolt transformation in the spring and emigrate at age 1, and the slowest growers remain in the stream for another year, again entering the maturation and emigration decision windows at their respective times.

The relevance of this framework for steelhead populations has not been previously assessed. There is evidence of at least moderate heritability of early maturation, smolting timing, and growth in steelhead (Thrower et al. in press), providing support for the concept of varying genetic thresholds for life history transitions. Here we focus on the environmental factors underlying the expression of different pathways. Although steelhead and Atlantic salmon share a similar repertoire of life history strategies and variability in those strategies, we believe the situation of steelhead in California is different. Atlantic salmon on a life history pathway of delaying emigration until age 2 reduce activity and feeding in winter, presumably as a means of reducing predation risk during a period of poor growth opportunity due to cold temperatures and low food availability. A similar response is evident in steelhead populations of Vancouver Island, where fish reduce growth rates in winter even when provided with elevated temperatures and unlimited food (Johnsson et al. 1993). Johnsson et al. (1993) suggested that high feeding activity in winter was maladaptive due to the associated risk and costs. However, for some California populations it is winter, rather than summer, that is the good growing season and summer may be the harshest season, from the perspective of growth (Merz 2002, Fig. 2). Thus, the timing of life history decisions in southern populations of steelhead is not necessarily comparable to Atlantic salmon, despite their similarity of plasticity in life histories. Models developed for Atlantic salmon may be more applicable in current form to northern populations of steelhead, which experience much harsher winter conditions. Furthermore, steelhead populations within California may experience very different biogeographic conditions. For example, preliminary studies of the four systems to be examined in this study found extreme differences in early growth rates and likely proportions of age-1 emigrants between the central coast and Central Valley. Development of appropriate life history models will require detailed comparisons of contrasts between the two regions. Most of our knowledge of steelhead ecology has been derived from northern populations. However, local adaptation of steelhead appears to be extensive; high levels of genetic differentiation among stream systems has been observed for both the Central Valley (Nielsen et al. 2003) and along the entire coast of California (Garza 2004). Thus, we expect to see many contrasts between California steelhead and northern residents, as well as contrasts among streams within California

The central role of early growth in determining life history trajectories provides a tractable means of generating the empirical data necessary to develop life cycle models for California steelhead and for using these models to understand the effects of water policy on steelhead population dynamics. Our overall focus is to understand the mechanisms underlying variability in potential growth rates and how different factors impact growth and consequent life history pathways. As outlined below, we believe management decisions affecting the growth environment, including habitat availability, food delivery via drift, and physical conditions such as temperature, can dramatically alter the natural distribution of life history patterns exhibited in steelhead populations. Development of appropriate, well-supported life history models for steelhead will be useful for both improved management of water resources for threatened populations and improved predictive capabilities for future environmental impacts such as global warming and drought regimes.

A notable exception in which California steelhead have been intensively studied is the analysis of Waddell Creek fish in the 1930s and 1940s (Shapovalov and Taft 1954). This detailed account provides invaluable data on variability in the proportions of different life history pathways over a ten year time period in a relatively pristine system on the central coast. For example, based on scale analyses of returning adults, approximately 10% of individuals surviving to adulthood migrated to sea in their first year, with most survivors emigrating at age 2 (69%) or age 3 (19%) (Fig. 3). Although their results from a downstream migrant trap did not directly measure emigration (many fish caught moving downstream may actually have remained in the creek another year), they are suggestive of a proportion higher than 10% for fish entering the ocean at age 1. Mortality rates of salmonids in general appear to increase immediately after ocean entry and are size-selective, with smaller fish less likely to survive (Ward and Slaney 1988, Holtby et al. 1990, Beamish and Mahnken 2001). Because size at emigration increases with freshwater age, individuals emigrating at older ages are more likely to survive the initial period of ocean residence (Ward and Slaney 1988). In Central Valley populations such as the American and Mokelumne rivers, growth during the first year is markedly higher than in central coast populations (Merz 2002, Fig. 2), likely resulting in a high proportion of fish emigrating at age 1 (Titus, unpublished data). The proportion of age-1 emigrants prior to dam construction and extensive habitat alteration in these systems is unknown. Clearly a significant trade-off is evident between survival to age 2+ in freshwater and size-selective survival upon ocean entry. Individuals remaining in the stream for a second year of growth must survive through the highly variable flow conditions present in winter. Likewise, emigrating fish must survive the initial gauntlet of predators awaiting them as they enter marine habitats.

Preliminary results:

In field collections of age-0 steelhead in Soquel Creek, we have not observed the bimodal size distributions in fall/winter that seem common in Atlantic salmon. Thus, this population does not appear to split into two life history trajectories prior to winter. Based on our direct measurements of growth rates (Fig. 2) and indirect estimates based on size-frequency distributions, growth in Soquel Creek is inhibited in summer but increases during winter/spring, opposite to the pattern typical of more northern populations of steelhead (Johnsson et al. 2003) and Atlantic salmon (Thorpe et al. 1998). Similar reversed seasonal patterns of growth have been observed in Scott Creek (Sean Hayes, NMFS, unpublished data), and Merz (2002) observed higher gut fullness levels in winter than other seasons for steelhead in the Mokelumne River. In academic year 2002-03, two of us (Mangel and Sogard) sponsored a senior thesis student who conducted preliminary studies in the lab examining some of the ideas of the life history models developed for Atlantic salmon by Thorpe et al (1998). On the theoretical side, the framework of Thorpe et al (1998) was modified, based on a literature review (Fig. 4). The results (Atcheson 2003) demonstrate the expected size relationship with spring $Na^{+}K^{+}$ATPase levels but unexpected patterns of behavior of non-emigrating fish (Fig. 5). Fish that were initially large in size (>130 mm in January) had significantly higher ATPase levels in April than smaller fish (< 100 mm in January), suggesting a higher probability of smolt transformation and emigration. One result was that low ration levels appeared to reverse the life history decision for some large fish. For large fish held on high rations, 76% had ATPase levels > 3.0, our index of seawater readiness, in contrast to 43% for large fish held on low rations. None of the small fish had elevated levels of the gill enzyme. General behavioral activity during the winter was predicted to be lower in small fish than in large fish based on the assumption that fish selecting a non-emigration pathway would reduce activity and aggression in winter as a risk avoidance strategy. However, Atcheson (2003) found that small fish had higher activity levels than large fish, suggesting continued searching for prey and no evidence of the near torpor observed in non-emigrating Atlantic salmon. Overall, these results emphasize that we need to modify the Atlantic salmon models for southern steelhead populations.

Goals, Objectives and Hypotheses

The overall goal of our proposed research is to extend the framework developed by Thorpe et al. (1998) for Atlantic salmon to California steelhead, using field and lab studies to derive appropriate empirical data and modeling to modify and refine the theory for Central Valley and central coast populations and apply it to investigate the effects of different flow regimes on steelhead population dynamics. In this manner, we will provide a tool that can be used to plan water management and enhancement of natural production of salmonids. We assume that smolt transformation and subsequent emigration depend on the physiological state of an individual at some time in advance of the actual initiation of the required physiological transformations; once this decision is made an individual fish is committed to a particular developmental pathway. In Atlantic salmon and potentially in northern populations of steelhead, this decision window is in the late summer or early fall, and greatly influences winter growth and behavior for individuals depending on the selected life history trajectory (emigrating in the spring or staying in the stream for another summer). For southern populations, we hypothesize that local adaptation results in a shift in timing of the emigration decision window. Shapovalov and Taft (1954) suggested that on Waddell Creek growth rates of juvenile steelhead declined in late summer due to high water temperatures and low flows, remained low through the winter flooding period, then rapidly increased in spring as temperatures increased and food delivery remained high. Recent tagging studies on the central coast (Scott and Soquel creeks) similarly demonstrate very slow growth rates in summer and fall, and accelerated growth in the winter/spring, when temperatures are mild and food availability presumably increases due to higher flows. Thus, the decision to emigrate likely occurs much closer to the actual start of transformation processes compared to populations that undergo harsh winters with minimal growth potential.

Growth rates of age-0 fishes are presumably driven by the interactions of several factors, including density of conspecifics and potential competitors, water temperature, genetic differences in growth capacity, and food availability. Diet analysis of juvenile steelhead captured in the American and Mokelumne Rivers has documented relationships of feeding activity with temperature and flow rates (Merz and Vanicek 1996, Merz 2000). We hypothesize that variability in water flow is a major determinant of variability in food availability through the impact on delivery of insect prey, resulting in a direct relationship of flow with growth potential. Drifting terrestrial invertebrates are a rich and preferred prey type for juvenile steelhead, and increase in abundance as water velocity increases (Smith and Li 1983). Poff and Ward (1989) emphasize the importance of stability in flow patterns for the productivity of stream fish. Seelbach (1993), for example, found that stable flows were associated with high survival of steelhead through their first winter. Management decisions that alter the natural patterns of flow rates thereby have the potential to alter growth rates and, consequently, life history pathways of steelhead. For example, if the emigration decision window occurs prior to a period of normally high flow, disruption of food delivery may have a negative impact on fish that have adopted an early emigration trajectory. We do not know of any data linking these growth components on a seasonal basis and thereby addressing the issue of growth potential for steelhead in different seasons. Central Valley and central coast steelhead populations are likely to differ in life history patterns as a consequence of different environmental conditions in the two regions.

Hypotheses to be tested:

Our work in the laboratory will be guided by the following hypotheses:

H1: Life history pathways of early maturation, emigration and non-emigration are established during specific time periods (decision windows) in the first year of life.

H2: Growth rates and body condition during the decision windows establish the life history pathway selected by an individual fish.

H3: Timing of the decision windows differs among populations.

H4: Altered temperature regimes during the decision window influence the proportion of fish adopting different life history pathways.

H5: Behavior during winter months varies as a function of life history pathway and temperature.

The field work will be guided by the following hypotheses:

H6: Age-0 steelhead exhibit bimodal size distributions in the winter, reflecting a split into emigrating and non-emigrating trajectories.

H7: Availability of insect prey differs among stream systems and seasonally.

H8: Prey delivery via drift is a function of flow rate.

H9: Growth of age-0 steelhead is an interactive function of temperature, prey density, and competitor density.

Models will be developed concomitantly with the laboratory and field work, so that the empirical studies provide insight for formulating the models and data for parameterizing the models and so that the models provide detailed predictions that can be tested. Examples of this interplay between empirical and modeling work can be found in Clark and Mangel (2000), Chapters 4 and 5.

Plan of work: *Lab component*

Laboratory experiments will address the following questions:

1. When does the decision window for emigration occur?
2. How does the timing of the decision window vary among populations?
3. How does variability in winter temperatures modify the emigration decision?
4. How does fish behavior in winter vary as a function of life history trajectory?
5. Is early maturation of parr controlled by a similar decision window?

We will examine these processes in two populations of steelhead representing two contrasting environmental regimes. Scott Creek, on the central California coast, typifies an unmodified coastal system with low summer flows leading to poor summer growth conditions and mild winters when growth potential improves. A conservation hatchery operated by the Monterey Bay Salmon and Trout Project on a tributary of Scott Creek propagates steelhead for release in Scott Creek and a limited number of nearby creeks with depleted steelhead runs. Only wild fish returning to Scott Creek are used as spawners, ensuring minimal genetic alteration and domestication (sensu Price 2002) in the progeny. In the Central Valley, Coleman National Fish Hatchery propagates steelhead on Battle Creek. Genetic studies have concluded that these fish are closely related to fish from the upper Sacramento River and its tributaries (Nielsen et al. 2003), and thus are representative of populations in the northernmost Central Valley. These populations presumably experience the coldest winters within the Central Valley ESU, although still comparably mild compared to populations in the northern part of the species range. We predict that these two populations will differ in the timing of life history decisions as a function of their local adaptation to contrasting environmental regimes. As a consequence, behavioral responses to different winter temperatures are also likely to vary.

Standard egg and sperm removal and incubation procedures will be conducted by hatchery staff at each location, using aggregated males and females to ensure a varied mix of lineages within each population. Under a cooperative agreement with each hatchery, we will collect progeny just prior to the first feeding stage and transport them to our aquarium facilities at the NMFS Santa Cruz lab for subsequent growth experiments. The fry will likely be ready for transfer some time in May. This timing will allow us to have full control over the food availability experienced by different treatments of fish. In the laboratory, fish will be randomly assigned in groups of 20 fish to one of four treatments, with two replicate tanks for each. The two source populations will be maintained separately throughout the experiment. Treatments will vary the timing of a period of rapid growth, simulating fluctuating exposure to high food availability in a stream. All fish will be constrained to a moderate but continual growth rate via limited rations. Then, for a two-month period, the fish will receive unlimited rations, allowing rapid increases in growth. Prior studies in our lab have demonstrated a marked capacity in the Scott Creek population to capitalize on these feeding opportunities with accelerated growth rates (exceeding 1 mm d^{-1}), and we expect the Coleman population to respond similarly. Following the two-month fast growth opportunity the fish will be returned to restricted rations for the remainder of the experiment. The four treatments will be comprised of enhanced growth in August/September, October/November, December/March, or February/March. We expect the decision window to be limited to one of these periods, and fish experiencing rapid growth during this window will adopt an emigration strategy, with full seawater readiness in April/May.

Fish will be maintained under a natural photoperiod intermediate to Scott Creek and Battle Creek latitudes. In year one, temperatures will be varied on a daily basis to match typical seasonal patterns of Scott Creek (mild winter temperatures). In year two, the experiment will be repeated using a temperature regime comparable to the average pattern on Battle Creek (colder temperatures). Results of the two experiments will provide additional information on the effects of temperature on the decision window and behavior patterns of the two populations. Our objective is to match the natural physical conditions of the two systems but manipulate the timing of growth opportunities. Food provided will be a standard hatchery pellet, BioDiet, with pellet sizes continually increased as fish grow into appropriate sizes.

Growth will be monitored by measuring and weighing all fish on a monthly basis during restricted feeding and bi-weekly during the period of high rations. Rations will be adjusted accordingly to maintain the desired growth trajectories. Behavior of fish in each treatment will be examined in late winter and early spring to determine any differences associated with life history trajectory and temperature regime. Pairs of fish from each tank will be placed in circular tanks with overhead video cameras and filmed for 4-hour periods during the day and at night. A PVC shelter will be placed in the middle of the tank. General motor activity, shelter use, and aggressive interactions will be quantified and compared among treatments and between day and night. Our preliminary results using these methods with the Scott Creek population have suggested that fish selecting a non-emigration pathway (at age 1) do not reduce activity in the winter (Fig. 5), in contrast to results for Atlantic salmon (Metcalfe 1998). However, the northern California population from Coleman Hatchery, which typically has much colder winters, may be more likely to behave similarly to Atlantic salmon.

We expect fish on a life history trajectory leading to emigration in the spring to exhibit changes in physiological state as they prepare for smolt transformation. Smolting fish typically have lower condition indices, increased silvering, increased metabolic rates, and increased activity levels compared to non-smolting fish (Folmar and Dickhoff 1980). We will use a combined index of these factors to identify individuals likely to smolt in the spring. Condition indices will be calculated at each measurement interval. Fish will be photographed periodically throughout the experiments to assess changes in coloration. We will monitor physiological condition of the fish in our experiments by measuring swimming capability and metabolic rate in a swim tunnel respirometer once a month, using a representative sample of fish from each population and treatment. We predict that metabolic rates will increase for individuals that have entered the emigration trajectory (Forseth et al. 1999). Fish will be tested individually in a tunnel respirometer, with respiration measured after 30 min of acclimation at a moderate swimming speed of 3 body lengths s^{-1}. A series of four randomly selected fish from each of the 8 population/ration treatments will be tested each month.

In late April, the expected time of emigration for all fish in the emigration life history pathway, gill filament samples will be collected for Na+K+ATPase enzyme analysis (McCormick 1993). After a one week recovery period from gill sampling, fish will receive a seawater challenge to assay their ability to osmoregulate in full strength seawater. Fish will be transferred directly from freshwater to seawater at a salinity of 32 ppt and left for 48 hours. Individuals will be scored as smolts or non-smolts depending on their ability to survive and maintain equilibrium in seawater. Seawater readiness will be compared with Na+K+ATPase levels to verify the ability of the enzyme assay to accurately predict smoltification. Seawater readiness will be equated with a decision to emigrate at age-0 and compared across factors of population source and ration treatment. We predict that fish exposed to high food availability during the appropriate decision window will exhibit a greater likelihood of seawater readiness than fish experiencing poor growth conditions during this decision window. Fish in the latter groups will presumably select a non-emigration pathway and will fare poorly in seawater challenges. At the conclusion of the experiment all fish will be sacrificed and dissected to determine early maturity. Mature parr are not expected to exhibit characters associated with smolting and will be excluded from treatment comparisons for determination of the decision window.

In year 3 we will focus on factors leading to early maturation of parr. Pre-feeding fry will be obtained from the two respective hatcheries and held in laboratory tanks as in years 1 and 2. We hypothesize that early maturation is induced by rapid growth rates during a decision window that precedes the emigration decision window (Thorpe et al. 1998). Manipulation of food availability influences early maturation in brown trout *Salmo trutta* (Pirhonen and Forsman 1999). Accordingly, fish will be maintained on ad libitum diets up to a selected time period, then fed a restricted ration for the remainder of the experiment. Treatments will shift from ad libitum to restricted diets at the end of July, September, or November. A control group will receive continuous ad libitum rations. If early maturation is turned on by a developmental switch during a specific time window, we predict that those individuals will mature in the early spring, regardless of their feeding success subsequent to the decision window. At the end of February, in the middle of the normal steelhead spawning period, all fish will be sacrificed and dissected to determine gender and stage of maturity.

Field component

Field studies will focus on evaluating seasonal patterns in growth potential for steelhead populations in four different watersheds, two in the Central Valley and two on the central California coast. Central Valley systems will consist of the American River, a tributary of the Sacramento, and the Mokelumne, which flows into the Sacramento-San Joaquin delta system. On the central coast, we will conduct studies in Soquel and Scott creeks, both of which flow directly into the Pacific Ocean, passing through small estuaries/lagoons that are typically blocked from ocean access during summer months due to sandbars. Prior research has indicated vastly different growth rates of age-0 steelhead at the regional level, but similarities between the two streams within each region. Within each stream system we will establish four 100 m reaches for sampling. Our focus will be to select sampling sites that cover a range of conditions and habitats currently being used by age-0 *O. mykiss* in each system. Our goal is to examine the variability in growth potential as a function of different environmental conditions and to document the breadth of responses exhibited in natural systems by young steelhead. Physical parameters of temperature and flow will be monitored on a continuous basis. Temperatures will be recorded using Onset TidBits placed in housings at each site. Water flow data will be obtained from USGS records available for 3 locations on the American River and 1 location on Soquel Creek. Flows at the 16 individual sampling sites will be periodically calibrated against USGS values with a hand held stream flow meter.

The diet of age-0 and age-1 steelhead is comprised primarily of insect larval and adult stages (Merz & Vanicek 1996). We expect availability of these prey to be highly variable depending on seasonal cycles of production and fluctuating delivery via drift. Documenting seasonal patterns of food abundance will be a key component of our field research and one of the most time intensive efforts. It is also a vital information gap, as relatively little effort has been expended to address the annual variability of prey in natural steelhead waters (or any salmonid, for that matter). Insect prey for young steelhead is derived from in situ (benthic) sources and delivered via drift from upstream sources. To sample these two components we will use benthic samplers (Surber or modified Hess) and stream drift nets, deployed according to standard protocols. Collected organisms will be identified to broad taxa and categorized as potential prey for either age-0 or age-1 steelhead. Dr. Joe Merz (EBMUD) has agreed to assist us with training in identification of stream invertebrates, and processing of benthic and stream samples will take place in his laboratory. Sampling will be conducted at the 16 sites on a seasonal basis (four time periods per year). In addition, we will examine variability in food availability on a diel basis by sampling across a 48 hour time period at one site in each stream and each season. To provide more detailed comparisons of prey abundance with flow rates, we will conduct sampling on an opportunistic basis as water flows vary within a season. We expect this variability to be expressed primarily during fall and winter in association with rainstorms. Standard parametric statistics will be used to evaluate differences in food abundance across regions, streams within regions, and as a function of season and flow rate.

Fish density estimates, steelhead size distributions, and the species composition of potential predators and competitors will be determined using snorkeling observations at two sites within each stream. Standard snorkeling transects will be conducted along the 100 m reach during four time periods (spring, summer, fall, winter) each year. Abundance and size distribution of *O. mykiss* and other fish species present in each reach will be recorded. Roni and Fayram (2000) found that nighttime observations provided estimates comparable to electrofishing for small salmonids, whereas daytime snorkeling underestimated abundance, particularly at low water temperatures (small fish are more likely to feed at night and hide during the daytime). We will conduct preliminary tests to determine if night snorkeling counts exceed day counts and plan further sampling accordingly. When low flow rates restrict snorkeling capabilities, as is likely in summer for the coastal streams, density estimates will be supplemented with electrofishing. A series of depletion sampling with 3 passes of the shocker will be completed when necessary to complement snorkeling efforts. For Central Valley systems, low water clarity may inhibit snorkeling surveys. In this case, the fish community will be sampled with seines and trawls to provide a coarse estimate of fish density and potential competitors and predators.

Growth rates will be monitored indirectly using the time series of length-frequency estimates derived from density sampling and directly using mark and recapture methods at the same eight sites. In late spring/early summer of each year, steelhead will be caught via seining or electroshock fishing. Fish < 65 mm FL (all presumed to be age-0) will be tagged with different colors of fluorescent elastomer (Northwest Marine Technology) in a series of 10 mm size classes. Fish > 65 mm will be tagged with PIT (Passive Induced Transponder, Allflex corporation) tags, which provide a unique identifier for each individual. Subsequent recaptures at each sampling site during the four seasonal efforts will provide data on growth rates within each season. As fish attain the 65 mm target, they will be PIT tagged, providing increasing sample sizes for tracking of individual growth rates. These methods have proven to be highly effective in evaluating growth in one of our systems, Soquel Creek (Fig. 2).

Emigration of PIT tagged steelhead from Scott Creek is currently being monitored by the Salmon Ecology Team, NMFS Santa Cruz, using a stream wide antenna/reader system with continuous logging as tagged individuals move past the reader. We will collaborate with these researchers to detect movement of fish tagged in this study, and will construct a similar system in

Soquel Creek. Although current antenna systems for the smallest PIT tags are limited to a relatively small passage area, we expect that continued development of this technology will allow us to design a reader suitable for use on the American and Mokelumne Rivers. If feasible, we will use these readers to continuously monitor movement of tagged fish out of the respective streams. Timing of emigration will be compared with age, size and growth data for tagged steelhead.

All of the field studies will be conducted across the full 3 years of the project. We expect to encounter a broad range of environmental conditions across this time, providing the opportunity to evaluate the maximum variability in growth potential experienced by natural steelhead populations in the four watersheds. This intensive effort will provide a wealth of data on the physical environment, food availability, and fish density across seasons in four different stream systems. Growth rate measurements will elucidate the interactive effects of these factors and any population differences potentially attributable to local adaptation. We expect to see markedly different results between the two broad regions of Central Valley and central coast. All results will feed directly into the modeling component of this project as they become available.

Modeling component

The modeling component of our work has four main goals:

1) To modify the theory of Thorpe et al. (1998) to account for the unique biogeography (for salmonids) of California, including frequency dependence.

2) To apply this theory to steelhead trout by appropriate parameterization of the timing of the life history windows and the estimation of the thresholds from a combination of literature review and connection to laboratory and field experiments conducted in the course of this project.

3) To explore the fitness consequences of steelhead developmental plasticity (sensu Bateson et al. 2004), so the consequences of individual life history patterns can be scaled to the population.

4) To use the theory to address the CalFed priority topic area of how water operations are related to biological resources and the CVPIA objective of doubling naturally producing salmonids.

The theory of Thorpe et al. (1998) recognizes that salmonid life histories are characterized by two primary developmental conversions (Smith-Gill 1983), smolting and sexual maturation. In Atlantic salmon, although smolting occurs in the spring, the critical decision at which physiological decisions are taken occurs in mid-summer. The framework is one in which a fish is assumed to project a measure of size and condition at the time of smolting with a genetically determined threshold (Fig. 1).   If the projection is greater than the threshold, then the fish commits to a developmental pathway leading to smolting; otherwise it is resident in freshwater another year. The timing of this process in Atlantic salmon was confirmed in independent studies using appetite (Metcalfe et al 1986, Huntingford et al. 1988), body growth (Thorpe et al. 1989), and otoliths (Wright et al. 1990). This process leads to diversity in life histories, and generates the great diversity in life histories of Atlantic salmon. Similar diversity is seen in the life history of steelhead trout (Shapovalov and Taft 1954). Furthermore, this theoretical framework leads us to understand that each salmonid migration (Egg ---> Gravel redd, Redd --> Stream bed, Stream bed --> Feeding territory, Feeding territory --> Downstream, Freshwater ---> Sea) is an abandonment of a habitat that can no longer satisfy the needs of the fish. That is, steelhead trout migrate because the freshwater environment is insufficient for them, not because the ocean is good for them. This is confirmed, for example, in studies of growth rates of steelhead and rainbow trout (Johnsson et al 1993).

To develop a computationally practicable description of the developmental switches, proximate mechanism, and fitness consequences requires the following components:

a) A growth model to characterize the anticipated and actual trajectories. An initial framework can be developed from existing models (Weatherley and Gill 1981, Weatherley and Gill 1995, West et al. 2001, Forseth et al. 2001, Elliott et al. 1996, Elliott 1994, Hill and Grossman 1993), parameterized initially with the data in Shapovalov and Taft (1954) and refined through our own empirical work. These models are typically of the form $\frac{dW}{dt} = q\Phi(T(t))W^a - \alpha e^{0.071T(t)}W^b$ where W(t) is mass at time t, q is maximum food assimilation efficiency and related to the abundance of food, $\Phi(T(t))$ characterizes the temperature dependence of food assimilation, a and b are allometric parameters (a=2/3, b=1 corresponds to von Bertalanffy growth), and α is a measure of standard metabolic rate. We will make such general models specific to steelhead, separating coastal and Central Valley fish.

b) A measure of relative performance. This measure compares the actual and anticipated performance over the decision window used by the fish. For steelhead, we do not know the timing or the length of the window, and the empirical work will determine those. Given those, a natural measure of relative performance is the relative specific growth rate (e.g. actual divided by anticipated). We will assume that length is given by an allometric relationship with weight, determined by our empirical studies.

c) Projection to the time of smolting. We will iterate the growth model forwards in time, from the end of the assessment period to the time of smolting. Once the growth model is set, this is straightforward.

d) Comparison of the projected size at the time of smolting and the genetically determined threshold. We will use the empirical work, plus literature reviews, to determine information about the distribution of the thresholds for smolt metamorphosis. This is a relatively complicated inverse problem, in which we observe the distribution of growth rates and life history pattern and infer the thresholds.

e) Computation of expected reproductive success. Reproductive success has components of survival and reproduction. Salmonids, and fish in general, have mortality rates with size dependent and size independent components and the size dependent component scales inversely with mass to approximately the 1/3 (Lorenzen 1996); we will use mortality $m(W) = m_0 + m_1 W^{-0.37}$, where m(W) is the mortality rate of a fish of mass W and m_0 and m_1 are the size independent and size dependent components of mortality. By combining the growth and survival models, and comparing them with survival data, we will be able to estimate these parameters. We will follow the procedure of Mangel (1996) for computation of female fitness from smolt size; this procedure relies on a combination of literature based parameters and our empirical work. The situation with males is more complicated, since salmonid males have two main reproductive strategies: Larger males fight for access for females, while smaller males 'sneak' matings at the time that a larger male is mating (Gross 1985, Gross 1991, Gross and Repka 1995, Aubin-Horth and Dodson 2002). In the extreme, male parr that have grown very well will mature in freshwater and attempt such matings. This behavior is currently understood in the context of conditional strategies related to a threshold (Hazel et al. 1990, Gross and Repka 1995, Aubin-Horth and Dodson 2002, Hazel et al. 2004) and thus generally consistent with the framework of Thorpe et al (1998). Although the theory of Thorpe et al (1998) did not account for early maturation in males, we will do so for steelhead.

f) Forward projection of survival, size, reproductive success and population dynamics in relation to flow. The maximum food assimilation efficiency q and water temperature at time t, T(t), behave in predictable and understood relations with respect to water flow (e.g., reduced flow, all else being equal, will reduce q and increase T). Consequently, we will be able to use the model to predict the consequences of changes in flow at different times of the year on the growth, survival and smolt metamorphosis of juvenile steelhead and on the population dynamics of steelhead.

Project Justification

Intellectual Merit

Attachment 1 of the Science Program 2004 Call for Proposals listed the topics that represent ‘what we need to learn to support short-and long-term decision making in CALFED’. These topics include 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. The work proposed here contributes to each of these topics.

Our project blends theoretical and empirical traditions in environmental science and will allow direct confrontation of models with data (Hilborn and Mangel 1997). We are focusing on the most complex of the salmonids in California because 1) the framework for Atlantic salmon exists and steelhead are in many senses the ‘closest’ Pacific salmonid, so that once we have developed a framework applicable to steelhead, the specification to chinook and coho salmon will be not too difficult and 2) our work will implicitly shed light on the anadromous/resident dichotomy in steelhead, one that is important for both applied and fundamental considerations (Hendry and Stearns 2004).

There are likely to be many interesting similarities and contrasts among the various populations in the Central Valley and on the central coast. Although our focus for this project will be on the factors influencing timing of life history transitions in anadromous individuals, the general framework will be relevant to addressing the resident vs. anadromous decision. Results of this study will provide valuable background information for future analysis of the factors influencing reversal of life histories (adoption of anadromy by progeny of resident *O. mykiss* and vice versa, (Zimmerman and Reeves 2000, Thrower et al. in press).

Management implications

The work outlined here will allow a better connection between water management decisions (particularly flow regimes) and predictions of individual growth, survival, and life history trajectories of steelhead and the consequences of those for population dynamics. Natural flow patterns in Central Valley rivers and streams have been greatly altered by water management operations. If flows play a major role in controlling growth rates of steelhead by modifying prey availability and temperature regimes, altered flow patterns likely influence life history strategies and the timing of decision windows. Better understanding of how environmental factors interact with internal state to determine emigration patterns will be beneficial in predicting timing of smoltification and any reversals of the decision to emigrate. As described in the body of the proposal, the management implications thus focus on two of the three CalFed priority topic areas and the CVPIA goal of increasing natural production of salmonids.

Dissemination of Results

We will publish our work in leading professional journals and put the papers on both the web site of Marc Mangel (http://www.soe.ucsc.edu/~msmangel/) and on that of the Center for Stock Assessment Research (http://www.soe.ucsc.edu/~msmangel/CSTAR.html). Members of our research team will attend appropriate scientific conferences to present the work.

Feasibility of plan of work

In our previous work, we have demonstrated feasibility of each component of the project (field studies, laboratory studies and modeling). Preliminary studies have been conducted for all major aspects and some results are illustrated here (Fig. 2, Fig. 5). Initial field results have provided clear evidence of broad variability in steelhead growth in the different systems, supporting the primary rationale for this project. Initial lab results have allowed us to fine tune experimental protocols for manipulating growth rates and measuring behavioral responses and physiological changes associated with smolting. The co-supervision of Ms. Megan Atcheson by Mangel and Sogard demonstrates the feasibility of linking theory with empirical studies.

Management of collaborators and conceptual model of combined projects

The groups led by Mangel and Sogard will have regular weekly meetings. During these meetings, we will discuss the details of the research project, have people present their results to date, and read relevant literature for the project. We will have two meetings per year with Titus, who will join us in Santa Cruz. Sogard will provide timely results of laboratory experiments to Mangel for incorporation into the modeling component and Mangel's team will provide predictions that can be tested in the laboratory or observed in the field. Titus and Sogard will participate jointly in field sampling and provide results to Mangel. Dr. Joe Merz, East Bay Municipal Utilities District, will collaborate on an informal basis, providing advice on appropriate sampling sites on the Mokelumne River, assisting with field work, and providing educational support for training in identification of potential steelhead prey items.

Budget

Empirical studies

Sogard will spend 30% of her time on this project at no cost to CALFED. The team supervised by Sogard will consist of one post-doc and one technician, to be housed at the NMFS Santa Cruz laboratory. The post-doc will supervise all lab and field components of the study. The technician will participate in all lab and field work and will be responsible for data collection and management in laboratory experiments and field studies. An additional technician will be supervised by Titus and will reside in his laboratory. This technician will participate in all field work and will be responsible for processing of all invertebrate samples. Travel funds are requested for travel to collecting sites by the full research team; we have budgeted for 8 trips per year. Growth and maturation experiments will be conducted using aquarium facilities provided by the Santa Cruz NMFS laboratory. Funds are requested for permanent equipment for a chiller to control water temperatures. Additional funds are required for expendable laboratory supplies and field collecting supplies.

Modeling

Mangel will spend 15% of his time during the academic year and one summer month on the project. The team working on the modeling side of the project will be lead by Mangel and will consist of a post-doctoral colleague (full-time) and a 50% BS-level post-graduate research assistant, who will aid with collection and organization of data, library work, and runs of the computer model once it is developed. We are also requesting funds for computers for the computations, and a modest amount for supplies and ancillary expenses.

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Policansky, D. 1983. Size, age and demography of metamorphosis and sexual maturation in fishes. American Zoologist **23**:57-63.
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Roni, P., and A. Fayram. 2000. Estimating Winter Salmonid Abundance in Small Western Washington Streams: A Comparison of Three Techniques. North American Journal of Fisheries Management **20**:683-692.
Seelbach, P. W. 1993. Population biology of steelhead in a stable-flow, low-gradient tributary of Lake Michigan. Transactions of the American Fisheries Society **122**:179-198.
Shapovalov, L., and A. 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 Fish Bulletin **98**:1-373.
Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. Pages 173-180 *in* D. L. G. Noakes, editor. Predators and prey in fishes.
Smith-Gill, S. J. 1983. Developmental plasticity: developmental conversion versus phenotypic modification. American Zoologist **23**:47-55.
Thorpe, J. E., C. E. Adams, M. S. Miles, and D. S. Keay. 1989. Some influences of photoperiod and temperature on opportunity for growth in juvenile Atlantic salmon, *Salmo salar* L. Aquaculture **82**:119-126.

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.

Thrower, F. P., and J. E. Joyce. in press. Effects of 70 years of freshwater residency on survival, growth, early maturation, and smolting in a stock of anadromous rainbow trout from southeast Alaska. American Fisheries Society Symposium.

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

Weatherley, A. H., and H. S. Gill. 1981. Recovery growth following periods of restricted rations and starvation in rainbow trout *Salmo gairdneri* Richardson. Journal of Fish Biology **18**:195-208.

Weatherley, A. H., and H. S. Gill. 1995. Growth. *in* C. Groot, L. Margolis, and W. C. Clarke, editors. Physiological Ecology of Pacific Salmon. University of British Columbia Press, Vancouver.

West, G. B., J. Brown, H., and B. J. Enquist. 2001. A general model for ontogenetic growth. Nature **413**:628-631.

Wright, P. J., N. B. Metcalfe, and J. E. Thorpe. 1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L.: evidence against coupling. Journal of Fish Biology **36**:241-249.

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

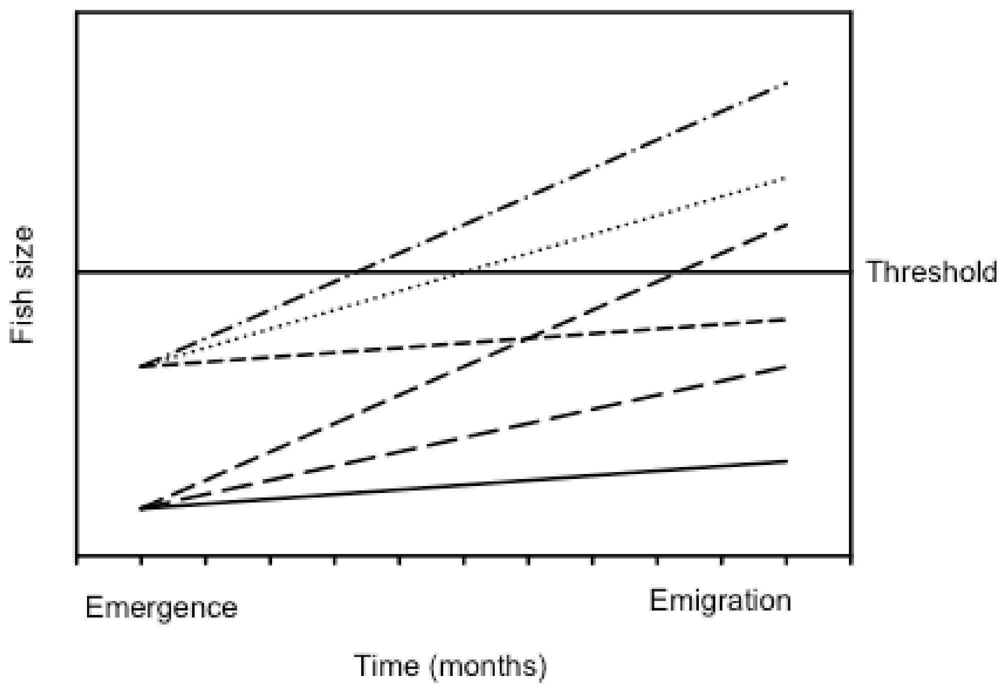


Figure 1. Life history decisions are made in response to a genetically determined threshold and environmentally induced condition. Fish emigrate when predicted size at the time of emigration crosses the threshold (shown here to be the same for all fish). Lines indicate trajectories of fish that differ in initial size and growth rate.

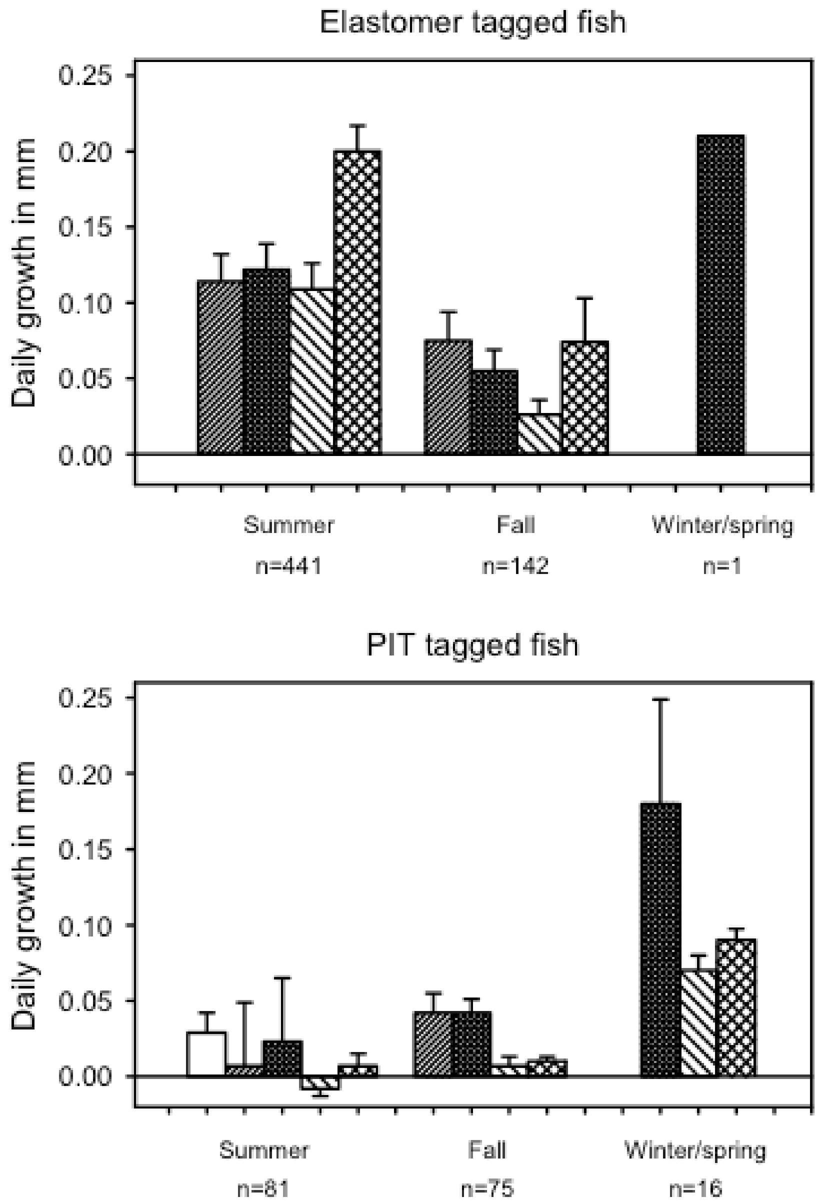
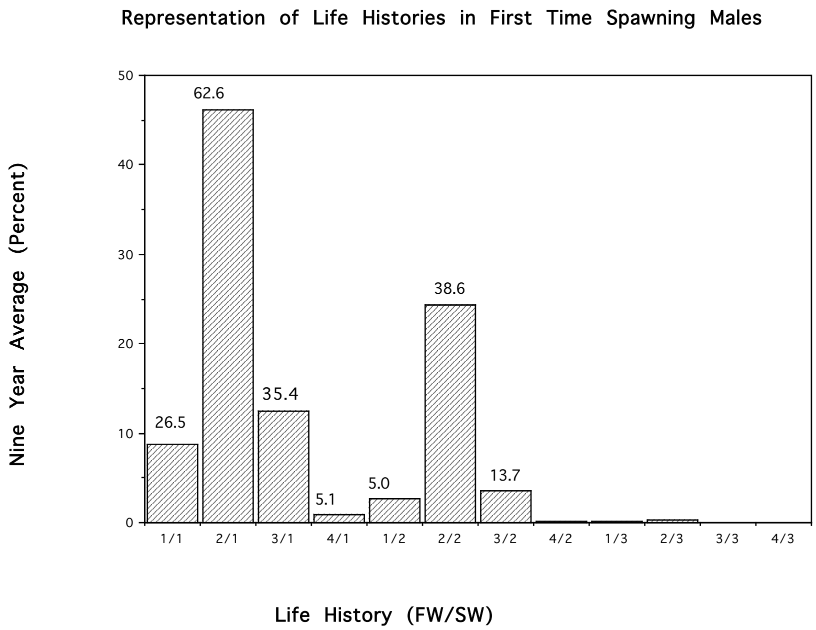


Figure 2. Mean growth rates (+ S.E.) of juvenile steelhead in Soquel Creek during 3 seasons. Fish were tagged in June 2003 with elastomer (fish < 80 mm) or PIT tags (fish > 80 mm) and recaptured in October 2003, December 2003, and June 2004. Hatch marks designate different sampling sites. Note that only a single elastomer tagged fish was recaptured in June 2004.



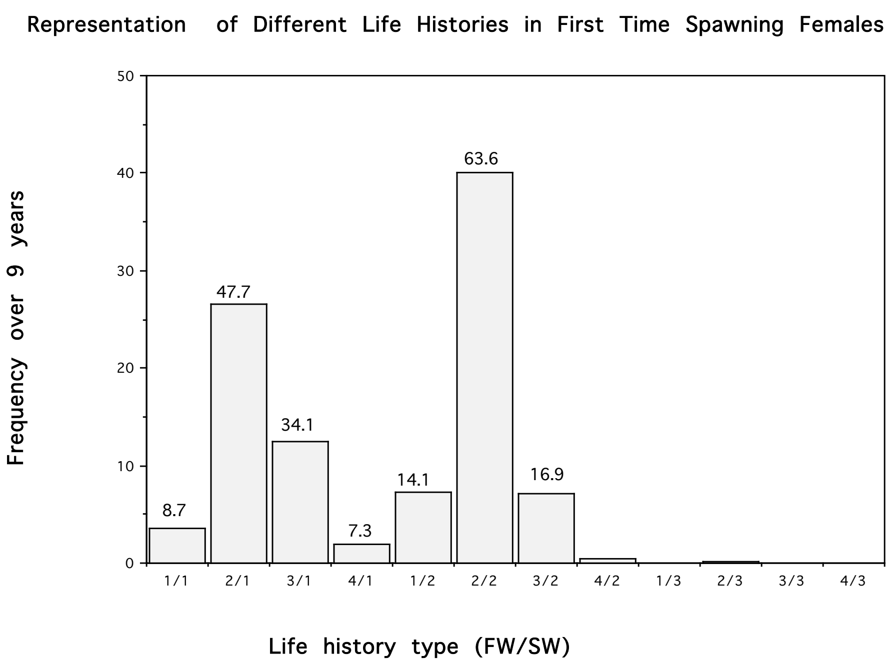


Figure 3. Representation of freshwater years and life history patterns of first time spawning males (upper panel) and females (lower panel) in Waddell Creek (data from Shapovalov and Taft 1954).

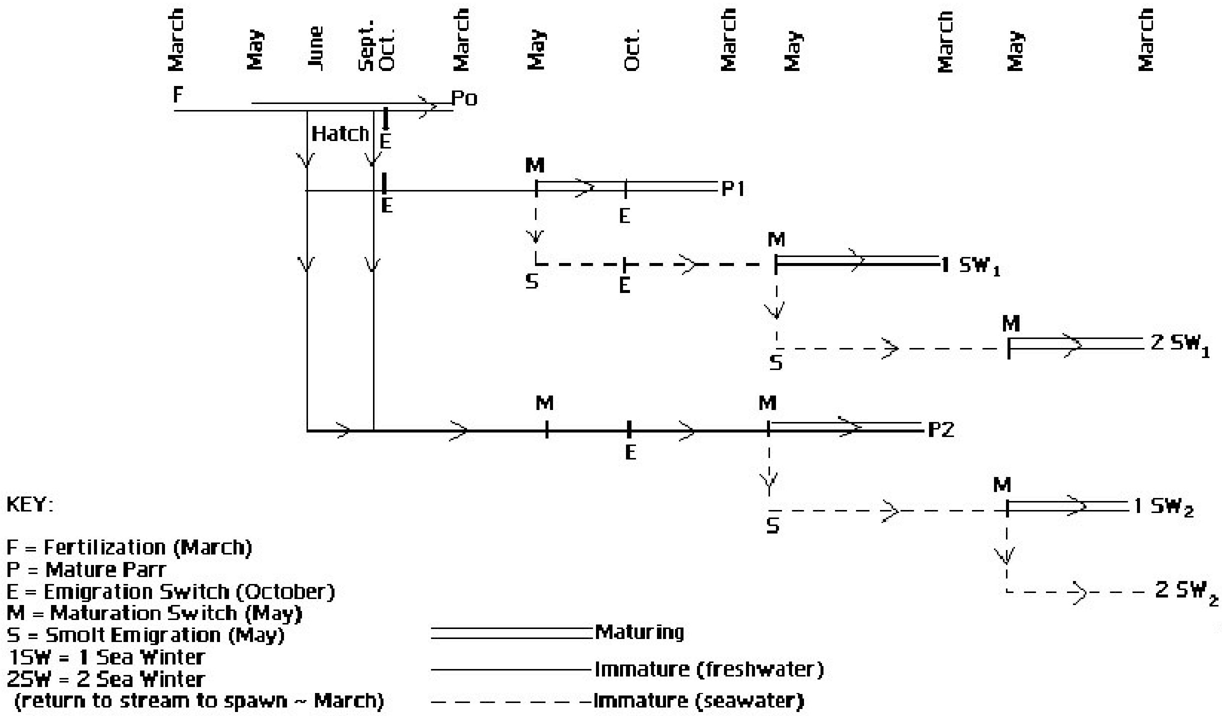


Figure 4. Preliminary modification of the life cycle diagram of Thorpe et al. (1998) for steelhead in California

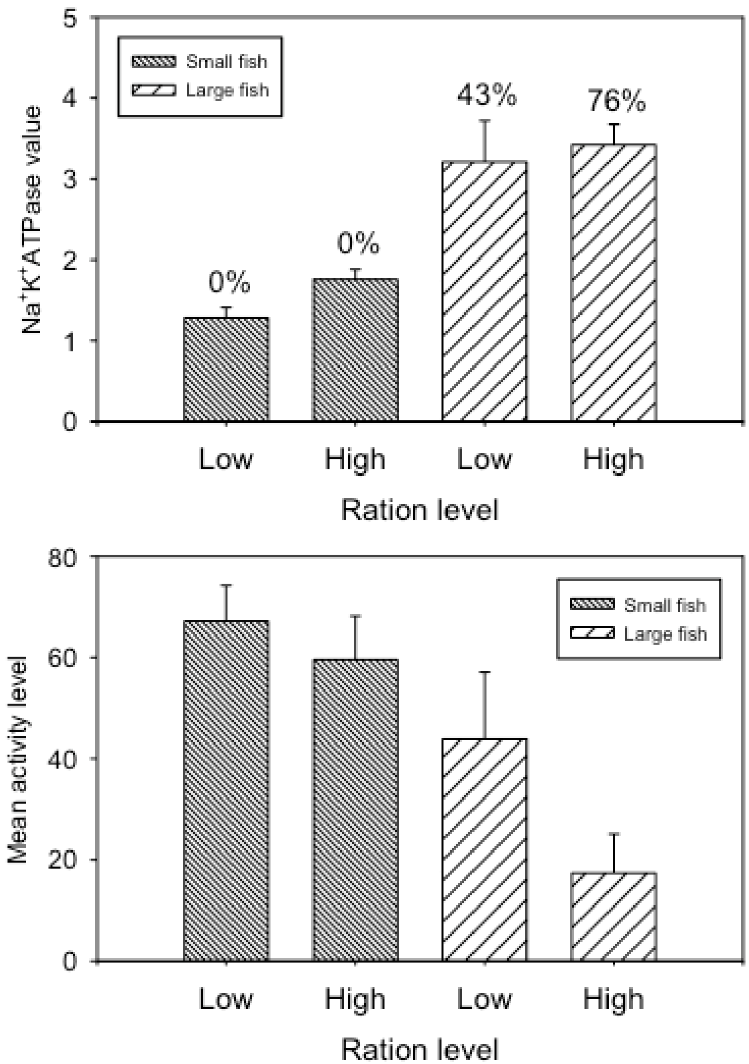


Figure 5. Mean (+ S.E.) Na+K+ATPase levels in April and mean (+S.E.) motor activity levels in March for juvenile steelhead that were initially small (<100 mm) or large (>100 mm) in January and maintained on low or high rations. Values above bars in upper figure are the percentage of fish in that treatment with ATPase values exceeding 3.0, the nominal index of smolt transformation.

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Birthdate: 10 March 1951

Citizenship: U.S.A.

EDUCATION

B.S. (Physics, High Honors), University of Illinois, 1971
M.S., (Biophysics) University of Illinois, 1972
Ph.D., (Applied Mathematics and Statistics), University of British Columbia, 1978

PERMANENT POSITIONS

Scientific Analyst, Center for Naval Analyses (CNA), 1977-80
[CNA is the Navy's federally funded research and development center. Its research activities include operations analysis, systems analysis, and system engineering]
University of California Davis (UCD): Assistant Professor 1980-82; Associate Professor 1982-84; Professor 1984-96
University of California Santa Cruz (UCSC), 1996-: Professor and Fellow of Stevenson College

<u>Major administrative duties and appointments:</u>

Co-founder (with R. Plant), Graduate Program in Applied Mathematics, UCD (1981-83)
Chair, Department of Mathematics, UC Davis 1984-1989
Co-founder (with J. Quinn, C. Toft, M. Turelli), Graduate Program in Population Biology, UCD (1986-89)
Director, Center for Population Biology, UCD 1989-1993
Director, Geographic Information Systems/Interdisciplinary Sciences Computational Laboratory, UCSC, 1996-1999
Associate Vice Chancellor, Planning and Programs, UCSC 1997-1999
MRAG Americas, Inc.
1999 – 2004, Senior Science Advisor
2004-present, Regional Director, California Office

HONORS AND AWARDS (selected)

Phi Beta Kappa, 1971
NIH Traineeship in Biophysics, 1971
Koopman Paper Prize, Operations Research Society of America, 1981
JASA-Applications Invited Paper, American Statistical Association, 1983
Fellow, John Simon Guggenheim Memorial Foundation, 1987
George Gund Foundation Distinguished Environmental Scholar,1992

Distinguished Statistical Ecologist, International Association for Ecology, 1998
Fellow, California Academy of Sciences, 2000
William R. and Lenore Mote Eminent Scholar Chair in Fisheries Ecology and Enhancement at Florida State University and the Mote Marine Laboratory, 2000
Fellow, American Association for the Advancement of Science, 2002

PANEL MEMBERSHIP (selected)

Participant, California Department of Fish and Game Workshop **Short-term Sardine Assessment and Management**, Tiburon September 1990
Member, Delegation of the United States to the **Scientific Review of Large-Scale Pelagic Driftnetting**, Sidney, BC, June 1991
Member, Delegation of the United States to the **Scientific Committee for the Conservation of Antarctic Living Marine Resources**, Hobart, Tasmania October 21-November 1, 1991
Member, Panel for the Review of the **US Antarctic Marine Living Resources Program**, May 1992
Member, Panel **Assessing Extinction Risk for West Coast Salmon**, National Marine Fisheries Service, November 1996
Member, **National Marine Fisheries Service Ecosystems Advisory Panel** (nominated by the National Research Council, NRC), 1997-2000
Member, **Delegation of the US to the CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) Working Group on Ecosystem Monitoring and Management**, July 1997, San Diego, CA
Member, **Review Team for "Issues to be Considered by the Evaluation Team for the Bering Sea and Gulf of Alaska Walleye Pollock Fishery**", National Fisheries Conservation Center, 2002
Member, **Review Team for "F40 Harvest Management Strategy"**, North Pacific Fisheries Management Council, 2002
Member, NOAA Fisheries **Recovery Science Review Panel** (NRC Appointment),2004-
Member, NERC (Natural Environment Research Council , United Kingdom) **Special Committee on Seals**, 2004-

EDITORIAL APPOINTMENTS (selected)

Member, Editorial Advisory Council, Natural Resources Modelling, 1984-1988
Associate Editor, Operations Research, 1987 -1992
Editorial Board, Ecological Applications, 1989-1994
Associate Editor, Theoretical Population Biology, 1989-
Editorial Advisory Board, Journal of Mathematical Biology, 1990-1999
Editorial Board, Evolutionary Ecology, 1991-1999
Editorial Advisory Board, Environmental and Ecological Statistics, 1992-
Co-Editor, Behavioral Ecology, 1994-1999
Editorial Board, Oecologia, 1998-2004
Editorial Board, Evolutionary Ecology Research, 1999-2004

PUBLICATIONS (selected)

Books and Edited Volumes

1985 Mangel, M. *Decision and Control in Uncertain Resource Systems.* Academic Press

1988 Mangel, M. and C.W. Clark. *Dynamic Modeling in Behavioral Ecology*. Princeton University Press.

1997 Hilborn, R. and M. Mangel. *The Ecological Detective. Confronting models with data*. Princeton University Press

2000 Clark, C.W. and M. Mangel. *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford University Press

Articles (selected, since 1994)

1994. Mangel, M. Climate change and salmonid life history variation. Deep Sea Research, II (Topical Studies in Oceanography) 41:75-106

1994. Mangel, M. Life history variation and salmonid conservation. Conservation Biology 8:879-880

1996 Bull, C.D., Metcalfe, N.B. and M. Mangel. Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. Proceedings of the Royal Society 263B:13-18

1996 Mangel, M. and 42 co-authors. Principles for the conservation of wild living resources. Ecological Applications 6:338-362 Republished with commentary in Environment Development Economics 2(1):40-110 (1997)

1996 Mangel, M. Life history invariants, age at maturity and the ferox trout. Evolutionary Ecology 10:249-263

1996 Castleberry, D.T., Cech, J.J., Erman, D.C., Hankin, D., Healey, M, Kondolf, G. M., Mangel, M., Mohr, M., Moyle, P.B., Nielsen, J., Speed, T.P. and J.G. Williams. Uncertainty and instream flow standards. Fisheries 21:20-21

1996 Mangel, M. Computing expected reproductive success of female Atlantic salmon as a function of smolt size. Journal of Fish Biology 49:877-882

1998 Thorpe, J.E., Mangel, M., Metcalfe, N.B. and F.A. Huntingford. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology 12:581-600

1998 Nonacs, P., Smith, P.E. and M. Mangel. Modeling foraging in the northern anchovy (*Engraulis mordax*): individual behavior can predict school dynamics and population biology. Canadian Journal of Fisheries and Aquatic Sciences 55:1179-1188

1998 Mangel, M. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. Ecology Letters 1:87-90

2001 Shea, K. and M. Mangel. Detection of population trends in threatened coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 58:375-385

2001 Mangel, M. and M.V. Abrahams. Age and longevity in fish, with consideration of the ferox trout. Experimental Gerontology 36:765-790

2001 Ludwig, D., Mangel, M., and B. Haddad. Ecology, conservation and public policy. Annual Review of Ecology and Systematics. 32:481-517

2002 Metcalfe, N.B., Bull, Colin D., and M.Mangel. Seasonal variation in catch-up growth reveals state-dependent somatic allocations in salmon. Evolutionary Ecology Research 4:1-11

2002 Mangel, M., Marinovic, B., Pomeroy, C., and D. Croll. Requiem for Ricker: Unpacking MSY. Bulletin of Marine Science 70: 763-781

2003 Munch, S.B., Mangel, M. and D.O. Conover. Quantifying natural selection on body size from field data: Winter mortality in *Menidia menidia*. Ecology 84:2169 2177

2004 Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D. Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J. and K.J. Sainsbury. Ecosystem-based fishery management. Science 305:346-347

2004 Ish, T., Dick, E.J., Switzer, P.V. and M. Mangel. Environment, krill and squid in Monterey Bay: from fisheries to life histories and back again. Deep-Sea Research II 51:849-862

2004 Cooper, A.B., Rosenberg, A.A., Stefansson, G. and M. Mangel. Examing the importance of consistency in multi-vessel trawl survey design based on the U.S. west coast groundfish bottom trawl survey. Fisheries Research 70:239-250

INVITED AND PLENARY LECTURES AT PROFESSIONAL MEETINGS (last five years, selected)

Plenary Speaker, CALFED Science Conference, October 2000

Plenary Speaker (Introductory Comments and Closing Talk), Third Mote Symposium in Fisheries Biology, October 2000

27th Annual Albert L. Tester Memorial Symposium Distinguished Speaker, University of Hawaii, March 2002

Plenary Lecture, University of Wisconsin Madison Ecology Group, 7th Annual Fall Symposium, October 2002

Opening Talk, Workshop on Linking Human Socioeconomic and Biophysical Processes in Benthic Marine Ecosystems Along the Pacific Coast in Baja California, Mexico. La Paz February 2003

Invited Talk, 27th Larval Fish Conference, Santa Cruz, CA, August 2003

Invited Talk, Symposium of the Conference, California Cooperative Oceanic Fisheries Investigations Annual Conference, November 2003

Invited Talk, Zoological Society of London Symposium on ‘Management of Marine Ecosystems: Monitoring Change in Upper Trophic Levels’, April 2004

Invited Talk, California Water and Environmental Modeling Forum Workshop on Using Models in Endangered Species Act Recovery Planning, September

Invited Speaker, Fifth William R. and Lenore Mote International Symposium “The Good, the Bad, and the Ugly: Integrating Marine and Human Ecology into Fisheries Management”, November

STUDENTS SUPERVISED

Thesis (Ph.D. unless otherwise noted) advisees and current position (+6 current)

J. Brodziak (Northeast Fisheries Center, Woods Hole, MA)
A. Bouskila (Department of Zoology, Beersheva University)
S. Gardner (Livermore National Laboratory)
J. Goulart (Portugese Government)
G.E. Heimpel (Department of Entomology, Univesity of Minnesota)
L. Karp (Department of Natural Resource Economics, University of California, Berkeley)
K. Little [M.S.]
B. Luttbeg (Kellogg Biological Station)
M. R. Maxwell (Southwest Fisheries Science Center, La Jolla, CA)
C. Peters (Bank of America, San Francisco) [M.S. and Ph.D.]
B. Phillips [M.S.]
A. Shelton (Florida State University)
S. Stefanou(Department of Agricultural and Rural Economics, Pennsylvania State University)
C. Wilcox (University of Adelaide, CSIRO, Hobart as of March 05)

Post-doctoral advisees in the last five years and current position (+1 current; lifetime total 22)

Suzanne Henson Alonzo (Assistant Professor, Yale University)
Moshe Kiflawi (Lecturer, Ben-Gurion University)
Stephan Munch (current, Assistant Professor, SUNY Stonybrook as of June 05)
Katriona Shea (Assistant Professor, Pennsylvania State University)
Melissa Snover (current, Staff Scientist, NMFS Pacific Islands Center as of February 05)

Curriculum vitae - Susan M. Sogard

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Education:
Ph.D. in ecology, October 1990, Rutgers University, New Brunswick, New Jersey.
M.S. in marine biology, July 1982, University of Miami, Miami, Florida.
B.S. (cum laude) in zoology and psychology, May 1977. Miami University, Oxford, Ohio.

Research interests:
Population dynamics and recruitment variability of early life history stages, life history strategies of fishes, essential fish habitats, growth variability in juvenile fishes, behavioral compromises and trade-offs in ecological requirements

Professional experience:

2001-present Supervisory Research Fishery Biologist, National Marine Fisheries Service, Santa Cruz, CA. As Ecology Branch Chief, responsible for supervising principle investigators, developing research programs, managing internal and external budgets, and coordinating collaborative projects within NOAA and with University researchers. Current research teams within the branch include Habitat Ecology, Salmon Ecology, Molecular Ecology, and Early Life History.

1994-2001 Research Associate, Oregon State University. Courtesy faculty position with the Department of Zoology. Assisted with teaching for graduate level courses, served on graduate student committees, advised students.

1993-2001 Oceanographer, National Marine Fisheries Service, Newport, OR. Research position involving design of experiments, coordination of field studies, supervision of technicians, and integration with other researchers in a program examining behavioral ecology of early juvenile fishes.

1991-1992 Postdoctoral Research Associate, Oregon State University, Newport, OR. Cooperative research position with the Behavioral Ecology program of NMFS. Responsible for field studies, laboratory experiments, data analysis and journal publication for studies of early life history in gadid fishes.

1984-1987 Research Biologist, National Audubon Society, Tavernier, FL. Director of ecological study of fish and decapod communities in Florida Bay. Involved planning research, writing grant proposals, analyzing data, writing papers for publication, supervising technicians and Earthwatch volunteers.

1983-1984 Biological Technician, National Marine Fisheries Service, Beaufort, NC. Responsible for data organization and analysis and writing publications on larval fish distribution and abundance in the Gulf of Mexico.

Professional societies:
Ecological Society of America
American Society of Ichthyologists and Herpetologists
American Fisheries Society (Western Division representative for the Early Life History Section, 1993-1994; Secretary 2000-2002)
Western Society of Naturalists

Review Panels: EPA EPSCoR program on human impacts and climate change, Louisiana Board of Regents (2000); Science Advisory Group of the Interagency Ecological Program on San Francisco Bay fisheries research (1999-2003); Higher Trophic Level Initiative, Florida Bay Research Program (1997); National Undersea Research Program Panel(1996); National Sea Grant Fisheries Panel (1993); EPA Global Climate Change Program (1992)

Proposal Reviewer for:
National Science Foundation; National Estuarine Research Reserve Program; National Undersea Research Program; California Sea Grant; Delaware Sea Grant; Florida Sea Grant; Mississippi-Alabama Sea Grant; University of New Hampshire/University of Maine Sea Grant; Gulf of Maine Regional Marine Research Program; Marine Fisheries Initiative (MARFIN); South Florida Ecosystem Restoration, Prediction, and Modeling program; Hudson River Foundation; National Marine Fisheries Service Cooperative Marine Education and Research Program; Saltonstall-Kennedy Program

Manuscript Reviewer for:
Journals: Bulletin of Marine Science; Canadian Journal of Fisheries and Aquatic Sciences; Copeia; Ecology; Ecological Applications; Environmental Biology of Fishes, Estuaries; Estuarine, Coastal and Shelf Science; Fisheries Oceanography; Fishery Bulletin; Journal of Experimental Marine Biology and Ecology; Journal of Fish Biology; Journal of the Marine Biological Association of the United Kingdom; Marine Biology; Marine Ecology Progress Series; Transactions of the American Fisheries Society; Wetlands

Book chapters: *Recent Developments in Fish Otolith Research* (editors D.H. Secor, J.M. Dean, and S.E. Campana); *Pacific Salmon and their Ecosystems: Status and Future Options* (editors D.J. Stouder, P.A. Bisson, and R.J. Naiman)

Book reviews:
Early Life History and Recruitment in Fish Populations (editors R.C. Chambers and E.A. Trippel), reviewed for *Environmental Biology of Fishes*

Graduate student committees:

Kirsten Grorud, Ph.D., Marine Biology and Fisheries, University of Miami
Stacey Harter, M.S., (graduated 2002), Marine Sciences, University of South Alabama
Glenn Almany, Ph.D., (graduated 2002), Zoology, Oregon State University
Karen Overholtzer, Ph.D., (graduated 2003), Zoology, Oregon State University

Michael Webster, Ph.D., (graduated 2001), Zoology, Oregon State University
Gonzalo Costillo, Ph.D., (graduated 2000), Fisheries and Wildlife, Oregon State University
Carol Seals, Ph.D., (graduated 2002), Fisheries and Wildlife, Oregon State University
William Pinnix, Ph.D., Fisheries and Wildlife, Oregon State University
Richard Wong, M.S., (graduated 2001), Marine Biology, University of Delaware

Service committees:

Larval Fish Conference, local committee for 27^{th} annual meeting, Program Chair, 2003
Hatfield Marine Science Center Distinguished Marine Scientist Colloquia, speaker selection committee, 2000-2001

Selected publications (out of 42):

Hurst, T.P., M.L. Spencer, S.M. Sogard, and A.W. Stoner. In press. Compensatory growth, energy storage and behavior of juvenile Pacific halibut *Hippoglossus stenolepis* following a thermally induced growth reduction. Mar. Ecol. Prog. Ser.

Berkeley, S.A., C. Chapman, and S.M. Sogard (2004). Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology 85:1258-1264.

Sogard, S.M. and M.L. Spencer. 2004. Energy allocation in juvenile sablefish: effects of temperature, ration and body size. J. Fish Biol. 64:726-738.

Sogard, S.M. and B.L. Olla. 2002. Contrasts in the capacity and underlying mechanisms for compensatory growth in two pelagic marine fishes. Mar. Ecol. Prog. Ser. 243:165-177.

Sogard, S.M. and B.L. Olla. 2001. Growth and behavioral responses to elevated temperatures by juvenile sablefish (*Anoplopoma fimbria*) and the interactive role of food availability. Mar. Ecol. Prog. Ser. 217: 121-134.

Sogard, S.M., K.W. Able and S.M. Hagan. 2001. Long-term assessment of settlement and growth of juvenile winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries. J. Sea Res. 45:189-204.

Sogard, S.M. and B.L. Olla. 2000. Effects of group membership and size distribution within a group on growth rates of juvenile sablefish *Anoplopoma fimbria*. Env. Biol. Fishes 59:199-209.

Sogard, S.M. and B.L. Olla. 2000. Endurance of simulated winter conditions by age-0 walleye pollock (*Theragra chalcogramma*): effects of body size, water temperature and energy stores. J. Fish Biol. 56:1-21.

Matheson, R.E. Jr., D.A. Camp, S.M. Sogard, and K.A. Bjorgo. 1999. Changes in seagrass-associated fish and crustacean communities on Florida Bay mud banks: the effects of recent ecosystem changes? Estuaries 22:534-551.

Sogard, S.M. and B.L. Olla. 1998. Contrasting behavioral responses to cold temperatures by two marine fish species during their pelagic juvenile interval. Env. Biol. Fish. 53:405-412.

Sogard, S.M. and B.L. Olla. 1998. Behavior of juvenile sablefish, *Anoplopoma fimbria* (Pallas), in a thermal gradient: Balancing food and temperature requirements. J. Exp. Mar. Biol. Ecol. 222:43-58.

Sogard, S.M. and B.L. Olla. 1997. The influence of hunger and predation risk on group cohesion in a pelagic fish, walleye pollock *Theragra chalcogramma*. Env. Biol. Fish. 50:405-413.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60:1129-1157.

Sogard, S.M. and B.L. Olla. 1996. Diel patterns of behavior in juvenile walleye pollock,

Theragra chalcogramma. Env. Biol. Fish. 47:379-386.
Sogard, S.M. and B.L. Olla. 1996. Food deprivation affects vertical distribution and activity of a marine fish in a thermal gradient: potential energy conserving mechanisms. Mar. Ecol. Prog. Ser. 133:43-55.
Olla, B.L., M.W. Davis, C.H. Ryer, and S.M. Sogard. 1996. Behavioral determinants of distribution and survival in early stages of walleye pollock, *Theragra chalcogramma*: a synthesis of experimental studies. Fish. Oceanogr. 5(Suppl. 1):167-178.
Sogard, S.M. 1994. Use of suboptimal foraging habitats by fishes: consequences to growth and survival. pp. 103-131 In: Theory and Application in Fish Feeding Ecology, D.J. Stouder, K.L. Fresh, and R.J. Feller (eds.), Belle W. Baruch Press, Columbia, SC.
Sogard, S.M. and B.L. Olla. 1993. Effects of light, thermoclines and predator presence on vertical distribution and behavioral interactions of juvenile walleye pollock, *Theragra chalcogramma* Pallas. J. Exp. Mar. Biol. Ecol. 167:179-195.
Sogard, S.M. 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. Mar. Ecol. Prog. Ser. 85:35-53.
Sogard, S.M. and K.W. Able. 1992. Growth variation of newly settled winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries as determined by otolith microstructure. Neth. J. Sea Res. 29:163-172.
Sogard, S.M., Powell. G.V.N., and J.G. Holmquist. 1989. Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida Bay mudbanks. Bull. Mar. Sci. 44:179-199.

Invited seminars and presentations:

Coastal fisheries research and policy: steelhead life history research. Annual Environmental Leadership Forum, STEPS (Science, Technology, Engineering, Policy, and Society) Institution for Innovation in Environmental Research, University of California, Santa Cruz, CA, June 2004.
Approaches to understanding life history strategies in juvenile steelhead. Symposium on Central Valley steelhead recovery, AFS Cal-Neva meeting, Redding, CA, April 2004.
Long term trends in estuarine habitat quality for newly settled winter flounder. Keynote speaker, International Flatfish Symposium, Atlantic Beach, NC, October 1999.
Size-selective mortality in the juvenile stage of teleost fishes: A review. AFS-ELHS symposium, Juvenile fish studies: contributions to early life history and recruitment processes. Seattle, WA, June 1997.
What's a hungry fish to do? Behavioral responses of juvenile walleye pollock to varying food levels. University of Alaska, Juneau, AK, November 1993.
Consequences of foraging in suboptimal habitats. Gutshop '92, a symposium on theory and application in fish food habits studies, November 1992 (session chair).
The influence of temperature stratification and food limitation on behavior, distribution and group cohesion in a juvenile pelagic fish. Symposium on Latitude and Temperature Effects, Ecological and Evolutionary Ethology of Fishes conference, June 1992.
Habitat quality comparisons for juvenile fishes in estuaries - an experimental approach. University of Washington, Seattle, WA, March 1992.
Fish utilization of seagrass meadows on Florida Bay mudbanks: spatial heterogeneity in distribution and abundance. Florida Bay Symposium, Miami, FL, June 1987.

Selected presentations (out of 46):

Rockfish reproductive strategies: larval condition vs. larval size. Western Society of Naturalists, Rohnert Park, CA, November 2004.

The importance of rapid growth for early life history stages of sablefish. 3rd International Symposium on Fish Otolith Research and Application, Townsville, Australia, July 2004.

Potential trade-offs in growth and lipid storage for juvenile sablefish. Early Life History Section/ Larval Fish Conference, Bergen, Norway, July 2002.

Contrasting mechanisms underlying compensatory growth in juvenile sablefish and walleye pollock. Early Life History Section/ Larval Fish Conference, Sandy Hook, NJ, August 2001.

Direct vs. indirect effects of global warming on temperate marine fishes. Marine Conservation Biology Institute symposium, San Francisco, CA, June 2001.

Strategies of energy allocation in juvenile sablefish. Early Life History Section/ Larval Fish Conference, Gulf Shores, AL, November 2000.

Growth and behavior responses to elevated temperatures in juvenile sablefish: implications for global warming. Western Groundfish Conference, Sitka, AK, April 2000, and American Society of Ichthyologists and Herpetologists meeting, La Paz, Mexico, June 2000.

Growth variability in juvenile sablefish (*Anoplopoma fimbria*): the roles of temperature and social interactions. Early Life History Section/ Larval Fish Conference, Beaufort, NC, April 1999.

A long-term study of settlement and growth patterns in young-of-the-year winter flounder in New Jersey estuaries. Flatfish Biology Conference, Mystic, CT, December 1998.

Risk balancing in juvenile fishes: factors modifying responses to predator threat. Gilbert Ichthyological Society meeting, Newport, OR, September 1996.

The consequences of size disparity on growth and behavior of juvenile sablefish. American Society of Ichthyologists and Herpetologists meeting, New Orleans, LA, June 1996.

Awards and honors:

Department of Commerce Bronze Medal (to FOCI researchers), 2001
NOAA Special Service Award, 1999, 2000, 2002, 2003
Stoye Award, best student paper, ASIH meeting, 1990
J. Frances Allen Scholarship, American Fisheries Society, 1990
Honorable mention, best student paper award, SEERS meeting, 1982
Top senior psychology major, Miami University, 1977
Elected to Phi Beta Kappa, Miami University, 1976

ROBERT G. TITUS

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CURRICULUM VITAE

EDUCATION

1991 PhD, Limnology, Uppsala University, Sweden. Dissertation: *Population regulation in migratory brown trout* (Salmo trutta)

1986 MSc, Biological Sciences, California State University, Sacramento. Thesis: *Comparative hooking mortality of Lahontan cutthroat trout at Heenan Lake, California*

1984–1985 Course work in limnology (24 semester units), Uppsala University, Sweden as participant in California State University International Program

1981 BA, Biological Sciences, California State University, Sacramento

POSITIONS

2004–present *Senior Environmental Scientist* (senior supervisor), California Department of Fish and Game, Stream Evaluation Program, Sacramento, California

2002–2004 *Staff Environmental Scientist* (senior specialist), California Department of Fish and Game, Stream Evaluation Program, Sacramento, California

1996–2002 *Environmental Specialist III*, California Department of Fish and Game, Stream Evaluation Program, Sacramento, California

1999–present *Lecturer*, Department of Biological Sciences, California State University, Sacramento (please see below for specific teaching assignments)

1996–present *Adjunct Professor*, Department of Biological Sciences, California State University, Sacramento

1993–1996 *Associate Fishery Biologist*, California Department of Fish and Game, Stream Evaluation Program, Sacramento, California

1992–1993 *Post-graduate Researcher*, Department of Forestry & Resource Management, (currently Environmental Science, Policy & Management), University of California, Berkeley

1987–1991 *Graduate Student Researcher/Lecturer*, Institute of Limnology, Uppsala University, Sweden

1986	*Fishery Biologist*, U. S. Bureau of Reclamation, Sacramento, California
1985	*Laboratory Assistant*, Institute of Limnology, Uppsala University, Sweden
1983–1984	*Biological Technician*, U. S. Bureau of Reclamation, Sacramento, California
1982–1983	*Graduate Student Assistant*, California Department of Water Resources, Delta Branch, Sacramento, California
1981	*Fish and Wildlife Seasonal Aid*, California Department of Fish and Game, Wild Trout Program, Rancho Cordova, California

TEACHING EXPERIENCE

Lecturer, Department of Biological Sciences, California State University, Sacramento

- Principles of Fishery Biology (**BIO 173**), fall 2000
- Advanced Fishery Biology & Management (**BIO 273**), spring 2004
- Conservation Policy and Administration (**BIO 270**), odd year springs 1999–2005
- Natural Resource Conservation (**BIO 118**), fall semesters 2001–2004

ARTICLES

Titus, R. G., M. C. Volkoff, and W. M. Snider. 2004. Use of otolith microstructure to estimate growth rates of juvenile Chinook salmon from a Central Valley, California stock. American Fisheries Society Symposium 39:181–202.

Titus, R. G. and H. Mosegaard. 1992. Fluctuating recruitment and variable life history of migratory brown trout, *Salmo trutta* L., in a small, unstable stream. J. Fish Biol. 41:239–255.

Titus, R. G. and H. Mosegaard. 1991. Selection for growth potential among migratory brown trout (*Salmo trutta*) fry competing for territories: evidence from otoliths. Can. J. Fish. Aquat. Sci. 48:19–27.

Titus, R. G. 1990. Territorial behavior and its role in population regulation of young brown trout (*Salmo trutta*): new perspectives. Ann. Zool. Fennici 27:119–130.

Titus, R. G. and H. Mosegaard. 1989. Smolting at age 1 and its adaptive significance for migratory trout, *Salmo trutta* L., in a small Baltic-coast stream. J. Fish Biol. 35 (Suppl. A):351–353.

Titus, R. G. and C. D. Vanicek. 1988. Comparative hooking mortality of lure-caught Lahontan cutthroat trout at Heenan Lake, California. Calif. Fish Game 74:218–225.

Mosegaard, H. and R. Titus. 1987. Daily growth rates of otoliths in yolk sac fry of two salmonids at five different temperatures. Pages 221–227 *in* S. O. Kullander and B. Fernholm (eds.). Proc. Fifth Cong. Europ. Ichthyol., Stockholm, 1985. Swed. Mus. Nat. Hist., Stockholm.

MANUSCRIPTS

Volkoff, M. C., R. G. Titus, and R. M. Coleman. Stock discrimination of Central Valley (California) fall-run Chinook salmon using otolith microstructure.

Titus, R. G., and C. E. Zimmerman. An integrated approach for characterizing individual life histories of steelhead rainbow trout. (in prep for submission to Calif. Fish Game)

Titus, R. G., and M. C. Volkoff. Life history diversity in Sacramento River (California) steelhead.

Titus, R. G., D. C. Erman, and W. M. Snider. History and status of steelhead in California coastal drainages south of San Francisco Bay. (~300 page monograph in manuscript)

TECHNICAL REPORTS

Snider, B., Reavis, B., R. G. Titus, and J. Lyons. *review draft*. Upper Sacramento River winter-run Chinook salmon escapement survey, May–August 2002. Calif. Dept. Fish Game, Habitat Conservation Division, Stream Evaluation Program Technical Report No. 05-01.

Snider, B., and R. G. Titus. 2002. Lower American River juvenile salmonid emigration survey, October 1998–September 1999. Calif. Dept. Fish Game, Habitat Conservation Division, Stream Evaluation Program Technical Report No. 02-02.

Snider, B., Reavis, B., R. G. Titus, and S. Hill. 2002. Upper Sacramento River winter-run Chinook salmon escapement survey, May–August 2001. Calif. Dept. Fish Game, Habitat Conservation Division, Stream Evaluation Program Technical Report No. 02-01.

Snider, B., and R. G. Titus. 2001. Lower American River emigration survey, October 1997–September 1998. Calif. Dept. Fish Game, Habitat Conservation Division, Stream Evaluation Program Technical Report No. 01-6.

Snider, B., and R. G. Titus. 2000d. Timing, composition and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1998–September 1999. Calif. Dept. Fish Game, Habitat Conservation Division, Stream Evaluation Program Technical Report No. 00-06.

Titus, R. G. 2000. Adult steelhead collected in the Calaveras River below New Hogan Dam in March 2000. Calif. Dept. Fish Game, Native Anadromous Fish Watershed Branch. Report prepared for Calif. Dept. Fish Game.

Snider, B., and R. G. Titus. 2000c. Timing, composition and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1997–September 1998. Calif. Dept. Fish Game, Habitat Conservation Division, Stream Evaluation Program Technical Report No. 00-05.

Snider, B., and R. G. Titus. 2000b. Timing, composition and abundance of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, October 1996–September

1997. Calif. Dept. Fish Game, Habitat Conservation Division, Stream Evaluation Program Technical Report No. 00-04.

California Department of Fish and Game (Titus, R., A. Vejar, and D. McEwan). 2000. Steelhead rainbow trout in San Mateo Creek, San Diego County, California. Calif. Dept. Fish Game, Native Anadromous Fish Watershed Branch and South Coast Region. Report prepared for National Marine Fisheries Service.

Snider, B., and R. G. Titus. 2000a. Lower American River emigration survey, October 1996–September 1997. Calif. Dept. Fish Game, Habitat Conservation Division, Stream Evaluation Program Technical Report No. 00-02.

Snider, B., R. G. Titus, and B. A. Payne. 1998. Lower American River, emigration survey, October 1995–September 1996. Calif. Dept. Fish Game, Environmental Services Division, Stream Evaluation Program Technical Report No. 98-6.

Snider, B., and R. Titus. 1998. Evaluation of juvenile anadromous salmonid emigration in the Sacramento River near Knights Landing, November 1995–July 1996. Calif. Dept. Fish Game, Environmental Services Division, Stream Evaluation Program Technical Report No. 98-5.

Snider, B., R. G. Titus, and B. A. Payne. 1997. Lower American River emigration survey, November 1994–September 1995. Calif. Dept. Fish Game, Environmental Services Division, Stream Evaluation Program Technical Report No. 97-3.

Vyverberg, K., B. Snider, and R. G. Titus. 1997. Lower American River, chinook salmon spawning habitat evaluation, October 1994. Calif. Dept. Fish Game, Environmental Services Division, Stream Evaluation Program Technical Report.

Snider, B., and R. Titus. 1996. Fish Community Survey, Lower American River, January through June 1995. Calif. Dept. Fish Game, Environmental Services Division, Stream Evaluation Program Technical Report No. 96-3.

Snider, B., and R. G. Titus. 1995. Lower American River, emigration survey, November 1993–July 1994. Calif. Dept. Fish Game, Environmental Services Division, Stream Evaluation Program Technical Report.

Titus, R. G. and H. Mosegaard. 1991. Multi-aged emigration of brown trout (Salmo trutta) in a small Baltic-coast stream: a mechanism for population persistence in an unstable environment. Page 20 *in* The Role of Aquaculture in Fisheries. Nordiske Jordbrugsforskeres Forening, Proc. from NJF seminar 194, Report No. 72.

Titus, R. G. 1984. San Luis Drain Report of Waste Discharge, Appendix A.3, Receiving and Supply Water Characteristics, Vol. III: Fishes. U. S. Bur. Reclam., Mid-Pacific Region, Sac., CA 141 p.

Titus, R. G., A. Pickard, and B. W. Collins. Effects of passage through low velocity fan pumps

on juvenile chinook salmon and American shad. Interagency Ecological Study Program for the Sacramento–San Joaquin Estuary, Technical Report (DRAFT).

SELECT GRANTS/CONTRACTS

- 2001–2005: U.S. Fish and Wildlife Service, $30,000 to *Comparative Growth of Central Valley, California Riverine and Delta Rearing Juvenile Chinook Salmon Based on Otolith Microstructure Patterns*. R. Titus, principal investigator.

- 1997/98–98/99: California Department of Water Resources and U.S. Fish and Wildlife Service, $25,000 per year to *Use of Otoliths to Evaluate the Role of Delta Rearing in the Life History of Central Valley Chinook Salmon and Steelhead.* R. Titus, principal investigator.

- 1997/98–98/99: East Bay Municipal Utility District, $31,000 to *Growth Rates of Juvenile Chinook Salmon in the Lower American River: Backcalculation using Otoliths*. R. Titus, P.I.

- 1992/93: California Department of Fish and Game, Environmental Services Division, $59,540 to *Status of steelhead trout in California, with emphasis on central and south coast stocks*. R. Titus, author, coapplicant with D. C. Erman.

SELECT RECENT PROFESSIONAL ACTIVITY

- On ongoing basis, referee manuscripts (#) for *Journal of Fish Biology* (2), *Transactions of the American Fisheries Society* (2), *North American Journal of Fisheries Management* (1), *California Fish and Game* (5), *Ecology* (1), and the proceedings of the first and second international symposia on otolith research and application (2)

- Presented, *Life History Diversity in Sacramento River Steelhead*, California Bay-Delta Authority Science Conference, Sacramento, CA, October 2004

- Presented, *Recruitment In Experimental Releases Of Brown Trout: Patterns In Dispersal And Survival Relative To Fry And Otolith Growth*, Third International Symposium on Fish Otolith Research and Application: Innovation and Implementation, Townsville, Queensland, Australia, July 2004

- Presented, *Use Of Otolith Microstructure To Estimate Growth Rates Of Juvenile Chinook Salmon From A Central Valley, California Stock*, 27th Annual Larval Fish Conference, Santa Cruz, CA, August 2003

- Presented, *What Do Analyses Of Carcass Survey Estimates, Screw Trap Catches, And Other Information Tell Us About Juvenile Winter-Run Chinook Production, Emigration Timing, And Factors Affecting Their Survival?*, CALFED-sponsored Environmental Water Account (EWA) Salmonid Workshop, California State University, Sacramento, July 2003

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Life History Variation In Steelhead Trout And The Implications For Water Mangement: Signature

This proposal is for the Science Program 2004 solicitation as prepared by Mangel, Marc Steven.

2004-11-04: In response to user feedback, some of the forms have been corrected and updated. Please read the current versions carefully.

The applicant for this proposal must submit this form by printing it, signing below, and faxing it to +1 877-408-9310.

Failure to sign and submit this form will result in the application not being considered for funding.

The individual signing below declares that:

- all representations in this proposal are truthful;
- the individual signing the form is authorized to submit the application on behalf of the applicant (if applicant is an entity or organization);
- the applicant has read and understood the conflict of interest and confidentiality discussion under the Confidentiality and Conflict of Interest Section in the main body of the PSP and waives any and all rights to privacy and confidentiality1 of the proposal on behalf of the applicant, to the extent provided in this PSP; and
- the applicant has read and understood all attachments of this PSP.

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

Proposal Number: 2004.01-0140

Submittor: Mangel, Marc Steven (msmangel@ucsc.edu)

Marc Mangel 22 Dec 04

Applicant Signature **Date**

MARC MANGEL UNIV. OF CALIFORNIA

Printed Name Of Applicant **Applicant Organization**

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