# Managing Natural Resources For Adaptive Capacity: The Central Valley Chinook Salmon Portfolio 

submitted to Science Program 2010 Solicitation
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Primary Investigator: Stephanie Carlson

## Project Information and Executive Summary

| Proposal Title | Managing natural resources for adaptive capacity: the Central Valley Chinook salmon portfolio |
| :---: | :---: |
| Primary Contact Organization Name | The Regents of the University of California |
| Primary Contact Organization Type public institution of higher education |  |
| Salutation of Primary Contact |  |
| First Name | Jyl |
| Last Name | Baldwin |
| Street Address | 2150 Shattuck Avenue, Suite 313 |
| City | Berkeley |
| State or Province | CA |
| Mailing Code | 94704-5940 |
| Telephone | (510)642-8109 |
| E-mail Address | spoawards@ berkeley.edu |
| Total Amount Requested | \$489,343 |
| Primary Topic Area | Native Fish Biology and Ecology |
| Secondary Topic Area(s) | Water and Ecosystem Management Decision Support System Development |
| Descriptive Keywords | economics; fish biology: salmon and steelhead; fish management and facilities: hatcheries; modeling: quantitative; natural resource management |
| Compliance statement | Our project will involve synthesis of existing data and dynamical modeling. Consequently, we do not anticipate that our project will require compliance of this nature. |
|  | $\begin{array}{ll} \text { Project Title: } & \text { Life History Variation In Steelhead Trout And } \\ \text { The Implicatio } \end{array}$ |
|  | Amount Funded: \$1,014,596 |
|  | Date Awarded: 15 February 2006 |
|  | Lead Organization: |
|  | Project Number: SCI-05-140 |
| Staff and/or subcontractors received funding for at least one project not listed above: | Project Title: $\quad \begin{aligned} & \text { Life History Variation in Management: } \\ & \text { Supplemental Grant App }\end{aligned}$ |
|  | Amount Funded: \$194,600 |
|  | Date Awarded: 1 July 2009 |
|  | Lead Organization: |
|  | Project Number: SCI-05-140 |

Primary staff applied for funding for at least one similar project
previously:

Recommend Reviewers

| Full Name | Organization | Telephone | E-Mail | Expertise |
| :--- | :--- | :--- | :--- | :--- |
| Ray Hilborn | University of <br> Washington | $206-543-3587$ | rayh@u.washington.edu | natural resource <br> management |
| Peter Moyle | University of California, <br> Davis | $530-752-6355$ | pbmoyle@ucdavis.edu | fish biology |
| Juha Siikamäki Resources for the Future | $202-328-5157$ | juha@rff.org | economics |  |
| Jeffrey <br> Hutchings | Dalhousie University | $+1-902-494-2687$ | Jeff.Hutchings@dal.ca | natural resource <br> management |

## Executive Summary

A diversity of phenotypes and dynamics among populations results in a variance-buffering "portfolio effect" (PE), wherein the variability of the population complex is less than that of individual populations. We propose to explore PE in Central Valley fall-run Chinook (CVC) by examining tradeoffs between multiple anthropogenic activities, including flow modification, hatcheries, and fisheries, investigating 1) the role of phenotypic diversity in contributing to PE, 2) effects of anthropogenic activities on PE, and 3) incorporating PE into management. To explore drivers of PE in this system, we will analyze stability and synchronization across time and space in existing time series data on population dynamics, environmental conditions, and anthropogenic activities. We will also model the relevant ecological, evolutionary, and economic drivers to explore how phenotypic diversity, environmental heterogeneity, and anthropogenic activities interact to determine overall system dynamics. We address Topic 1 with a focus on the protection and recovery of CVC. Our goal is to provide information on how various management actions are likely to affect PE in CVC and consequently resilience to environmental change. Thus, along with peer reviewed publications, we will develop quantitative tools (interactive spreadsheets, simulations) synthesizing dynamics relevant to a wide array of management domains (flow, hatcheries, fisheries) to support integrative management decision-making, Topic 4.

## Contacts and Project Staff

|  | Primary Contact |  |
| :--- | :--- | :---: |
| E-Mail | spoawards@berkeley.edu |  |
| Last Name | Baldwin |  |
| First Name | Jyl |  |
| Organization <br> Work | The Regents of the University of California |  |
| Telephone | $(510) 642-8109$ |  |
|  | Primary Investigator |  |
| E-Mail | smcarlson@berkeley.edu |  |
| Last Name | Stephanie |  |
| First Name | Carlson |  |
| Organization | UC Berkeley |  |
| Work | $510-643-9704$ |  |
| Telephone |  |  |
| Qualifications | See Appendix for complete CV of this Participant. |  |

## Participant \#2

| Salutation | Dr. |
| :--- | :--- |
| Last Name | Springborn |
| First Name | Michael |
| Title | Assistant Professor in Ecosystem Service Valuation |
| Organization | Davis, California University of |
| Position | Co-PI |
|  | PI Springborn will be responsible for contributing to all phases of evolutionary |
| Responsibilities | bioeconomic model and will take the lead on developing and analyzing the economic <br> dynamics of the model. |
| E-mail | mspringborn@ ucdavis.edu |
| Qualifications | See Appendix for complete CV of this Participant. |

## Participant \#3

| Salutation | Dr. |
| :--- | :--- |
| Last Name | Baskett |
| First Name | Marissa |
| Title | Assistant Professor in Quantitative Animal Conserv. Ecology |
| Organization | Davis, California University of |
| Position | Co-PI |
| Responsibilities | PI Baskett will be responsible for contributing to all phases of evolutionary bioeconomic take the lead on developing and analyzing the coupled |
| ecological-evolutionary dynamics of the model. |  |

## Participant \#4

| Salutation | Dr. |
| :--- | :--- |
| Last Name | Satterthwaite |
| First Name | William |
| Title | Assistant Research Applied Mathematician |
| Organization | Santa Cruz, California University of |
| Position | Co-PI |
| Responsibilities | PI Satterthwaite will be responsible for contributing to all phases of empirical analyses and |
| will take the lead on quantifying drivers of correlations and state-space modeling. |  |
| Qualifications | See Apterth@ soe.ucsc.edu |
| Spendix for complete CV of this Participant. |  |

## Participant \#5

Salutation Dr.

Last Name Lindley
First Name Steven
Title Ecologist, Landscape Ecology Team Leader
Organization National Oceanic and Atmospheric Administration
Position Co-PI
PI Lindley (unfunded) will share responsibility with PIs Carlson and Satterthwaite for the
Responsibilities time series modeling and will also provide guidance on the development of the evolutionary bioeconomic model.
E-mail Steve.Lindley@noaa.gov
Qualifications See Appendix for complete CV of this Participant.

## Participant \#6

| Salutation | Dr. |
| :--- | :--- |
| Last Name | Waples |
| First Name | Robin |
| Title | Senior Scientist |
| Organization | National Oceanic and Atmospheric Administration |
| Position | Co-PI <br> PI Waples (unfunded) will be responsible for guiding PIs Baskett and Springborn in |
| Responsibilities | developing the evolutionary bioeconomic model and will also provide guidance on the <br> empirical analyses. |
| E-mail | robin.waples @ noaa.gov |
| Qualifications | See Appendix for complete CV of this Participant. |

## Conflict of Interest

Primary Investigator Stephanie Carlson<br>To assist Science Program staff in managing potential conflicts of interest as part of the review and selection process, we requested applicants provide information on who will directly benefit if their proposal is funded, that were not listed on the Contacts and Project Staff Form.<br>Co-PI(s)<br>Subcontractor<br>Individuals who helped with proposal development<br>Last Name First Name Organization Role

## Task and Budget Summary

| Task \# | Task Title | Start <br> Month | End Month | Personnel Involved | Description | Task Budget |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | Administrative | 1 | 36 | Stephanie Carlson | This task includes, but is not limited to, cost verification, data handling, report preparation, and project oversight. | \$16,999 |
| 2 | Empirical <br> Analyses (UCB) | 1 | 36 | Stephanie Carlson; Dr. Steven Lindley | This task is devoted to synthesis and analysis of existing data. Note that we have partitioned our "empirical analyses" into two tasks, with task 2 representing the UC Berkeley portion of the budget. | \$145,350 |
| 3 | Empirical Analyses (UCSC) | 1 | 36 | Dr. William <br> Satterthwaite; Dr. Steven Lindley | This task is devoted to synthesis and analysis of existing data. Note that we have partitioned our "empirical analyses" into two tasks, with task 3 representing the UC Santa Cruz portion of the budget. | \$104,586 |
| 4 | Evolutionary <br> Bioeconomic Modeling | 1 | 36 | Dr. Michael Springborn; Dr. Marissa Baskett; Dr. Robin Waples | This task is focused on the development of an evolutionary bioeconomic model. | \$222,408 |
|  |  |  |  |  | Budget total | \$489,343 |

## Schedule of Deliverables

Each Science Program 2010 Solicitation grant recipient must provide the required minimum deliverables (listed below) for each project.

## Required minimum deliverables

- Semi-annual Progress Reports (due July 15 and January 15)
- Final Progress Report (Due at end of project)
- One page project summary for public audience at beginning of project
- One page project summary for public audience upon project completion
- Management implications of project findings
- Project closure summary report or copy of draft manuscript
- Presentation at Bay-Delta Science Conference
- Presentations at other events at request of Delta Science Program staff
- Copy of all published material resulting from the grant

| Additional deliverables | Description | Start <br> Month | End <br> Month |
| :--- | :--- | :---: | :---: |
| Manuscripts (empirical) on PE and drivers <br> submitted | Quantifying PE, identifying drivers, trends, <br> and viability | 1 | 36 |
| Code (empirical) for visualization | Commented R code for visualizing drivers <br> of PE and viability | 1 | 36 |
| Manuscripts (theoretical) on bioeconomic <br> model submitted | Understanding CVC dynamics and <br> management implications | 1 | 36 |
| Model code and decision-support <br> framework | Commented Matlab code for bioeconomic <br> model | 1 | 36 |

Note: This budget summary automatically links to the costs and totals on the "Budget Detail" worksheet. DO NOT CHANGE FORMULAS OR ENTER NUMBERS INTO ANY CELLS EXCEPT THE SHADED CELLS for "Cost Share" and "Other Matching Funds"

1/ Cost share funds are specifically dedicated to your project and can include private and other State and Federal
grants. Any funds listed in this line must be further described in the text of your proposal (see Chapter 3, Section D, of the PSP document)
2/ Other matching funds include other funds invested consistent with your project in your project area for which the ERP grant applicant is not eligible. Any funds listed in this line must be further described in the text of your proposal (see Chapter 3, Section D, of the PSP document)



1/ Indicate your rate, and change formula in column immediately to the right of this cell
1/ Indicate your rate, and change formula in column immediately to the right of this cell
No travel out of the state of California shall be reimbursed uniess prior written authorization is obtained from the State.
4/ Please provide a list and cost of major equipment ( $\$ 5,000$ or more) to be purchased, and complete "Equipment Det
4/ Please provide a list and cost of major equipment (\$5,000 or more) to be purchased, and complete "Equipment Detail" Worksheet
$6 /$ Please list each subcontractor and amounts (if subcontractor not selected yet, use function like "ditch construction subcontractor")
$7 /$ Indicate rate in column immediately to the right of this cell; and provide a description of what expenses are covered by overhead. If overhead is $>15 \%$ must provide justification

## Budget Justification - UC Berkeley (Carlson; Tasks 1 \& 2)

The budget will be applied towards conducting research detailed in the narrative, primarily to cover a portion of PI time dedicated to the project, travel to meet with co-PIs for collaboration, and travel to communicate and discuss results.

## Senior Personnel

Stephanie Carlson is the lead PI on this grant and thus will be responsible for the overall development and execution of the proposed research. Summer salary for Dr. Carlson will support administrative tasks ( $1 / 2$ month, including but not limited to cost verification, data handling, report preparation, and project oversight). The other $1 \frac{1}{2}$ months of summer salary will be devoted to advising of the graduate student, synthesis of data, time series modeling, manuscript preparation, and time presenting and disseminating results. Her focus will also include making connections from the data analyzed here with larger scale consideration of salmon populations on the West Coast. The budget thus includes two months of summer salary for each of three years for her contribution to this project.

## GSR Costs

Funding to support one Graduate Student Researcher (GSR) is requested and the GSR will be heavily involved in the proposed research. Under guidance from PI Carlson, the GSR will assist in data synthesis and analysis, and the research pursued under this grant will be the basis of the student's PhD thesis. Salary is requested for this GSR at $49.5 \%$ effort during one semester and the summer period across all three years. Funding for the second semester will come from a teaching assistantship at UC Berkeley.

## Fringe Benefits

Fringe benefits are assessed as a percentage of the respective employee's salary. The benefit rates are (1) Faculty summer rate $-12.7 \%$ and (2) GSR - 1.3\% (academic year rate) and 3\% (summer rate).

## Other Direct Costs

A total of $\$ 24,172$ is budgeted for the graduate student's fee remission (in-state fees), which is included in the other direct costs. Graduate students who are supported at $45 \%$ or more time are eligible for the full fee remission (including non-resident tuition). The budget reflects a $30 \%$ increase in tuition and fees for the first year (as currently proposed by UC administration) and a $10 \%$ increase in each successive year.

Publication charges to cover the cost of article submission to academic journals are included for years two and three.

A total of \$326,994 is requested to cover subawards to UC Davis (task 4) and to UC Santa Cruz (task 3).

## Travel

Travel expenses are intended to cover one national conference (e.g., American Fisheries Society) and one local conference (Delta Science Program) for Dr. Carlson and the Berkeley GSR.

National conference expenses (\$1750) are budgeted at four days including hotel ( $4 \times \$ 150$ ), conference fee ( $\$ 150$ ), food ( $4 \times 50$ ) and air/ground transportation ( $\$ 800$ ). Local conference expenses ( $\$ 500$ ) are budgeted at two days including hotel ( $1 \times \$ 150$ ), conference fee ( $\$ 150$ ), food ( $2 \times \$ 50$ ) and transportation (\$100).

## Indirect Costs

UC Berkeley's current negotiated Facilities and Administration rate exceeds the maximum allowed overhead rate by the DSP which is why the maximum indirect rate of $25 \%$ is applied to the Modified Total Direct Cost (MTDC). This MTDC is equal to the total direct costs excluding graduate student tuition and fees as well as the UC Davis and UC Santa Cruz subawards.

## Budget Justification - UC Davis (Baskett, Springborn; Task 4)

The budget will be applied towards conducting research outlined in the scope of work, primarily to cover a portion of PI time dedicated to the project, travel to meet with co-PIs for collaboration, and travel to communicate and discuss results.

## Senior Personnel

Summer salary for Drs. Springborn and Baskett will support advising of graduate students, modeling and simulation work, manuscript preparation, and time presenting and disseminating results. Salary is calculated on an 11-month base salary with an increase of $4 \%$ each year.

## GSR Costs

Drs. Springborn and Baskett will co-advise a GSR employed at $50 \%$ time for two quarters during the academic year and summer for three years. The GSR is budgeted at step III.

## Fringe Benefits

Fringe benefits are assessed as a percentage of the respective employee's salary. The benefit rates are (1) Faculty summer rate $-12.7 \%$ and (2) GSR - 1.3\% (academic year rate) and $3 \%$ (summer rate).

## Other Direct Costs

As required by UC Davis, we request funds to cover the cost of tuition and fee remission for the GSR. The budget reflects a 30\% increase in tuition and fees for the first year (as currently proposed by UC administration) and a $10 \%$ increase in each successive year.

Software expenses will include Matlab licenses for a PI and a student (2 x \$115 each year). Publication charges to cover the cost of article submission to academic journals are included for an ecological journal $(\$ 1,000)$ and an economics journal $(\$ 100)$ each year for years two and three.

## Travel

Travel expenses are intended to cover one local conference (Delta Science Program) and one national conference (e.g., American Fisheries Society) for Drs. Springborn and Baskett, as well as the GSR, over the 3-year period. Local conference expenses ( $\$ 500$ ) are budgeted at two days including hotel ( $1 \times \$ 150$ ), conference fee ( $\$ 150$ ), food ( $2 \times \$ 50$ ) and transportation ( $\$ 100$ ).

National conference expenses (\$1750) are budgeted at four days including hotel (4 x \$150), conference fee (\$150), food (4 x \$50) and air/ground transportation (\$800).

## Indirect Costs

UC Davis' current indirect cost rate agreement exceeds the maximum allowed overhead rate by the DSP which is why the maximum indirect rate of $25 \%$ is calculated on modified total direct costs to generate total indirect costs. UC Davis' current indirect cost rate agreement, dated August 29, 2008, can be viewed on line at:
http://www.research.ucdavis.edu/documentDisplay.cfm?id=1512,pdf.

## Budget Justification - UC Santa Cruz (Satterthwaite; Task 3)

The budget will be applied towards conducting research outlined in the project narrative, primarily to cover a portion of co-PI time dedicated to the project, supplies necessary for performing the work, and travel to communicate and discuss results.

## Senior Personnel

Principal investigator W. Satterthwaite (Assistant Research Applied Mathematician, Department of Applied Mathematics and Statistics, UC Santa Cruz) requests 25\% of salary (500 hours/year) and benefits. He requests travel funds to present results at one national meeting and one Delta Science Program Science Conference, and funds to cover page charges from resulting publications.

## Fringe Benefits

Total fringe benefits for Satterthwaite are calculated at 27\% of salary.

## Other Direct Costs

Direct costs will include books and software packages related to the application of novel techniques to our dataset, along with printing and miscellaneous office expenses (\$500 year 1, $\$ 250$ years 2 and 3 ).

Publication charges to cover the cost of article submissions to an ecological journal are requested for years two (\$500) and three (\$500).

## Travel

It is not year clear which year he will attend each conference, but expected costs are national conference expenses ( $\$ 1500$ ) budgeted at four days including hotel ( $4 \times \$ 100$ ), conference fee ( $\$ 100$ ), food ( $4 \times \$ 50$ ) and air/ground transportation ( $\$ 800$ ). DSP conference expenses ( $\$ 500$ ) are budgeted at two days including hotel ( $1 \times \$ 150$ ), conference fee ( $\$ 150$ ), food ( $2 \times \$ 50$ ) and transportation (\$100), so \$2,000 spread over two years.

## Indirect Costs

UC Santa Cruz's current indirect cost rate agreement exceeds the maximum allowed overhead rate by the DSP which is why the maximum indirect rate of $25 \%$ is calculated on modified total direct costs to generate total indirect costs for salary, supplies, publication, and travel costs.
COST SHARE CONTRIBUTIONS BY TASK

| TASK |  | JUSTIFICATION |
| :--- | :--- | :--- |
| Task 2: Empirical Analyses <br> (UCB) |  | AMOUNT |
| Carlson (UCB) | 0.5 months/year for FYs 2011, 2012, and 2013 |  |
| Lindley (NOAA) | 0.5 months/year for FYs 2011, 2012, and 2013 | \$13,599 |
| Task 3: Empirical Analyses <br> (UCSC) |  |  |
| Lindley (NOAA) | 0.5 months/year for FYs 2011, 2012, and 2013 |  |
| Task 4: Evolutionary <br> Bioeconomic Modeling |  | \$21,250 |
| Michael Springborn (UCD) | 0.5 months/year for FY 2012; 1 month/year for FY 2013 |  |
| Marissa Baskett (UCD) | 1 month/year for FYs 2011, 2012, and 2013 | \$17,039 |
| Robin Waples (NOAA) | 0.5 months/year for FYs 2011, 2012, and 2013 | \$22,729 |
|  |  | Total All Tasks: |

# Managing natural resources for adaptive capacity: The Central Valley Chinook salmon portfolio 

## 1 Project Purpose

Biodiversity across multiple ecological scales, from genes to ecosystems, plays a critical role in ecosystem function and the sustainable delivery of ecosystem services (Worm et al. 2006). In addition, diversity and heterogeneity comprise one of the key characteristics that determine the resilience of natural systems to environmental change (Levin and Lubchenco 2008). Traditional natural resource management has rarely incorporated the role of biodiversity in the decision-making processes, and doing so presents a set of new challenges and trade-offs for managers to consider. For example, management actions designed to enhance resource returns might have unintended consequences for biodiversity and hence the resilience of the system to future environmental change. This trade-off can pit anticipated short-term resource use returns from management activities against long-term biodiversity loss, imposing costs via threats to resource viability or stability (Worm et al. 2006). Design of effective decision support tools for natural resource managers needs to explicitly consider such long-run feedbacks between human and natural systems (Larkin 1996; Link 2002). Coherent management choice will therefore depend on integrating clearly stated ecological and economic goals.

Our proposed research will address the following central question: how do multiple anthropogenic activities interact with ecosystem processes to affect the ability of complex ecological systems to respond to environmental variation and change? To address this question, we will apply concepts borrowed from financial portfolio theory (Markowitz 1952). Specifically, our focus will be on the portfolio effect (PE, Doak et al. 1998), which is a variance buffering mechanism whereby the population variability in the aggregate of stocks (i.e., the portfolio) is less than the variability in individual stocks. Biocomplexity - or a diversity of phenotypes and life histories among individual stocks within a portfolio (sensu Hilborn et al. 2003) - contributes to asynchronous population dynamics, which then generates a stabilizing portfolio effect in a temporally heterogeneous environment (Schindler et al. 2010). Such biocomplexity has been observed in spatially-structured fish populations, including Pacific salmon (e.g., Hilborn et al. 2003; Isaak et al. 2003; Moore et al. 2010; Rogers and Schindler 2008; Schindler et al. 2010), Atlantic cod (Hutchinson 2008; Olsen et al. 2008), and herring (Secor et al. 2009; Kerr et al. 2010). Management approaches that maintain a diversity of stocks can buffer the variability in the aggregate because the relative contribution of different stocks to total production shifts as a function of the prevailing environmental conditions (Hilborn et al. 2003; Olsen et al. 2008; Rogers and Schindler 2008; Schindler et al. 2010), resulting in enhanced stability of harvest (Hilborn et al. 2003). The PE is thus a useful concept for managers to consider in that it accounts for adaptations to local conditions and phenotypic diversity across populations, incorporates resilience to environmental change, and considers feedbacks between human and natural systems.

Therefore, the PE concept describes an aggregate stock as a complex adaptive system (Levin and Lubchenco 2008), where the overall system response to environmental change depends on diversity, redundancy, and modularity among individual stocks and the feedback
between these characteristics in the natural system and anthropogenic activities. A critical component of this interplay is the degree to which anthropogenic activities affect heterogeneity within and between stocks through impacts on inter-stock connectivity and diversity. For example, in Pacific salmon systems, habitat loss has the potential to reduce or eliminate some life history components (McClure et al. 2008) and thus to reduce biocomplexity within the system.

Much of the current understanding of the PE in coupled human-natural systems focuses on a single dimension of the human system: fisheries. For example, the quintessential work on the consequences of biocomplexity is on the sockeye salmon stocks in Bristol Bay, Alaska. This fishery is considered an example of a sustainable fishery and recent research has revealed evidence of life history variation among (Hilborn et al. 2003) and within (Rogers and Schindler 2008) the major fishing stocks. The resulting PE then stabilizes the stock complex and the fisheries that exploit those stocks (Greene et al. 2010; Schindler et al. 2010). In stark contrast to Bristol Bay's diverse and productive salmon fishery is California's recently-collapsed Central Valley fall-run Chinook salmon (Oncorhynchus tshawytscha). Recent work suggests that the fall-run populations breeding in the different river systems are now genetically indistinguishable (Williamson and May 2005) and that hatchery-produced fish comprise roughly $90 \%$ of total production (Barnett-Johnson et al. 2007). The Central Valley fall-run Chinook, described in more detail in section 2 below, highlight the need for a deeper ecological and economic understanding of the complex interaction between the PE and multiple anthropogenic stressors.

### 1.1 Central questions

Here we propose to explore the PE given feedbacks and trade-offs between multiple anthropogenic activities, including water flow modifications, hatcheries, and fisheries, by focusing on the Central Valley fall-run Chinook portfolio. Specifically, we propose to examine this collapsed stock complex to explore the consequences of an anthropogenically-homogenized portfolio on natural and human systems. Through a comparative analysis that employs both synthesis of existing data and dynamical modeling, we will address the following questions:

1. Biodiversity, the PE, and environmental change: What is the role of different types of phenotypic diversity in PEs and the response of Central Valley fall-run Chinook salmon to environmental change?
2. Anthropogenic disruption of the PE: How do anthropogenic activities that affect salmon biocomplexity interact to influence the PE in a variable environment? How does this feed back into trade-offs between the different types of anthropogenic activities?
3. Incorporating the PE into management: What are the implications of recognizing PEs for management? How can management incorporate trade-offs between long-term anticipated benefits of enhanced biocomplexity and the potential sacrifices (opportunity costs) for human systems in the short-term?

Our framework will build capacity for making adaptive and integrative resource management decisions under changing conditions and uncertainty. In addition, we will explicitly
evaluate trade-offs between management decisions for water flow, hatcheries, and fisheries across temporal scales given our exploration of the impact of short-term resource (water and fisheries) use on the biocomplexity underlying the portfolio effect in CVC, and therefore on long-term sustainability.

## 2 Background and Conceptual Models

### 2.1 Pacific Salmon as a Model System for Examining PEs

Pacific salmon are structured into discrete breeding populations due to their natal homing behavior (Dittman and Quinn 1996). These reproductively isolated populations are then subject to local selection pressures, including the local biotic and abiotic conditions. Many fitness-related traits are heritable (Carlson and Seamons 2008), thus allowing for natural selection to drive adaptations to local conditions. The combination of natal homing and their use of diverse breeding and rearing habitats results in considerable inter-population variation in phenotypic traits (i.e., biocomplexity) and productivity. Dimensions of salmon life history variation that contribute to PEs include the age structure of outmigrating juveniles (termed 'smolts') and breeding adults, timing of migrations (downstream, upstream), size at migration, as well as egg size and fecundity. Just as inter-individual variation in phenotypic traits is fodder for selection acting within populations, inter-population variation is fodder for selection when the populations are mixed. Consequently, selection acts on each stock independently during some portions of their life history (e.g., juvenile rearing, breeding) but acts on the aggregate during other portions (e.g., ocean-rearing, ocean fishery).

### 2.1.1 Case Study: Collapsed Central Valley fall-run Chinook Salmon

In spring 2008, state and federal fishery managers imposed an emergency closure of commercial and recreational salmon fishing off the coasts of California and southern Oregon due to anticipated poor returns of Sacramento fall-run Chinook salmon, and the closure remained in effect in 2009. The closure represents the first in the fishery's 157 year history, and an estimated loss of $\$ 255$ million (La Ganga 2009). California's Central Valley Chinook salmon populations have been impacted by various anthropogenic activities (e.g., habitat loss, hatcheries, fisheries), all of which have likely contributed to biocomplexity loss in this system. This brings up novel questions about how to manage for maximal PE when anthropogenic activities extend beyond harvest as well as how to rebuild PE within stock complexes once it has been degraded. Managers are tasked with making choices over multiple controls - including flow operations, hatchery operations, and harvest - and under multiple, sometimes competing, social objectives.

We hypothesize that PE in CVC has been reduced by homogenization of both environments and salmon life histories. At the level of the environment, habitats in the Central Valley have become increasingly similar because of flow regulation, channelization, and restriction of salmon populations to low-gradient parts of rivers below barriers. In addition, hatchery rearing exposes a large portion of the fish in many rivers to a similar juvenile environment. Life history diversity has been reduced by the near-extirpation of all but
fall-run populations and potentially also by genetic homogenization due to hatchery production, straying, and population bottlenecks. We will therefore examine linkages between homogenization in biocomplexity-generating traits, environmental variability and change, and weakened PEs.

## 3 Approach and Scope of Work

To assess the interaction between anthropogenic and natural processes and changes in diversity among salmon stocks, we will explore the impact of phenotypic diversity on management goals with a combination of two approaches: syntheses of existing data and development of dynamical models. Below we describe the methods for each approach and how we will use the results to address the central questions described above.

### 3.1 Syntheses of Existing Time Series

### 3.1.1 Time Series Data

> Objective 1: Explore central questions 1 and 2 from an empirical perspective by quantifying the variation, synchronization, and stability in CVC across space and time.

To understand how anthropogenic activities influence the expression of portfolio effects in the impacted stocks, we will compare metrics of stock performance across the complexity hierarchy from individual stocks to the aggregate of stocks (i.e., the portfolio). Within the context of Central Valley fall-run Chinook, this will involve comparing adult returns from individual river systems, to the two main river basins (Sacramento vs. San Joaquin), to the entire Central Valley. Our hypothesis is that Central Valley Chinook will show evidence of a homogenized portfolio, which will be indicated by highly synchronous dynamics across the complexity hierarchy and a consequent weakness in the stabilizing PE.

All analyses will be based on estimates of total adult returns for fall-run Chinook salmon to rivers in California's Central Valley. These numbers have been obtained from the CHINOOKPROD dataset, maintained by the US Fish \& Wildlife Service's Anadromous Fish Restoration Program, which can be found at: fws.gov/stockton/afrp/. We plan to restrict our analysis to nine rivers, representing both river basins, for which data are available for at least fifty years, including five populations from the Sacramento Basin (mainstem Sacramento, Battle, Feather Yuba, American) and four populations from the San Joaquin Basin (Mokelumne, Stanislaus, Tuolumne, Merced).

Although these data are not without measurement error, they are the best available and those that are used in status reviews of this stock complex (e.g., Williams et al. 2007). We have done simulations to quantify the effects (mostly minimal) of observation error on the analyses we propose (Carlson and Satterthwaite in review). While noise might cause us to overestimate the strength of the portfolio effect, noise primarily serves to obscure patterns and reduce our power to detect correlations among stocks-and it is these correlations that are the most interesting component to predicting how the strength of the portfolio effect will


Figure 1: Quantification of the portfolio effect in Central Valley fall-run Chinook. Panel (A) shows the mean coefficient of variation (CV) in adult returns for individual rivers, entire basins, and the entire Central Valley, (B) shows the effects of increasing the number of rivers pooled together on the resultant CV, and (C) shows the effect of basin and distance between river mouths on the pairwise correlations in river returns. Squares are San Joaquin Basin streams, circles are Sacramento Basin streams, and triangles (panel C only) are cross-basin comparisons.
change in response to various management activities. Thus, the patterns that we do detect tend to be ones that are robust and unlikely to be spurious.

### 3.1.2 Preliminary Results: Analysis, Integration and Synthesis of Existing Information, Native Fish Biology and Ecology

Our work on PE in fall-run Chinook to date (Carlson and Satterthwaite in review) has revealed that a weak portfolio effect remains in Central Valley fall-run Chinook despite its degraded state. Specifically, we found that some variance buffering was observed when comparing the coefficient of variation in adult returns in a given river basin to its constituent populations but not when comparing returns to the Central Valley as a whole to its constituent basins (Figure 1a,b) due to disproportionately many fish returning to the Sacramento Basin. We further explained our results in terms of the contribution each river makes to stabilizing the system based on both its average abundance and how correlated it is with the rest of the system, noting that correlations among rivers tended to be higher within basins than across basins (Figure 1c), while abundances were higher in the Sacramento than the San Joaquin. We also noted that correlations among rivers tended to be higher in years when abundances were low (results not shown). Thus we were able to demonstrate that, under current conditions, rivers in the San Joaquin contribute little to stabilizing the entire stock complex, despite lower correlations with the rest of the system, due to their low abundance. These results suggest equivalent investments in restoration of a river in the San Joaquin Basin would likely do more to stabilize the stock complex than in the Sacramento Basin,
although the exact effects would depend on how much abundance on that river was increased and how its correlation with other rivers was affected. We also repeated these analyses using an alternate dataset (GrandTab, also maintained by USFWS) and found qualitatively similar results to those reported above.

### 3.1.3 Planned Research: Native Fish Biology and Ecology

Applying these results in a management context requires a deeper understanding of what drives differences between rivers in adult returns, and the drivers in correlations across rivers. This knowledge will provide a means for generating the inputs for the management and visualization tools proposed in section 3.1.4.
3.1.3.1 Drivers of abundance To explore potential processes driving variation in adult returns, we will integrate our data on returns with indices derived from historical records of water flow, water temperature, and hatchery production (when applicable) on each river along with indices of ocean conditions and harvest rate. We will then use multivariate approaches such as ordination to characterize annual returns within each river, the two basins, and the Central Valley as a whole, to explore the degree to which various environmental indices and the amount of hatchery production can explain variation in annual returns. Here our goal is to extract patterns in the data, rather than testing a priori hypotheses.
3.1.3.2 Drivers of across-river correlations We hypothesize three main drivers of across-river correlations, whose relative strengths we will estimate. First, correlations among rivers might result from variations in local (river-specific) conditions that are nonetheless similar among rivers. Using flow records assembled over the time series for which we have run size estimates, we will test the degree to which correlations between rivers in their flow rates predicts correlations between rivers in their run size dynamics. To do this, we will first calculate cross-correlations between all pairs of rivers in their flow rates. We will then assign pairs of rivers a distance score based on how decoupled their flow rates are, and use a Mantel test to estimate the degree to which similarity in flow rates predicts similarity in run size dynamics (see also Rogers and Schindler 2008). Realizing that much hatchery production is trucked to the Bay directly, and thus effects of flow on production in hatchery-dominated streams might be less apparent, we will perform this analysis for (1) all rivers and (2) the subset of rivers without hatcheries.

Second, correlations among rivers might reflect environmental bottlenecks that are directly shared across some but not all rivers. For example, fish emigrating from the San Joaquin must all pass through the southern Delta, which is considered a more dangerous outmigration route (Brandes and McLain 2001), while fish emigrating from the Sacramento Basin must all pass through the northern Delta. We will compile records of pumping activity and water levels in the Delta (ideally generating separate indices for the northern and southern portions) and examine how correlations among rivers in different years track changes in Delta conditions across those same years. Again, we realize that hatchery production largely bypasses the Delta. Thus, we will also explore the effects of outplanting strategies in synchronizing dynamics across watersheds, over both ecological and evolutionary time scales. Life history diversity within and among stocks can provide further buffering beyond that
produced by independent dynamics (Schindler et al. 2010). We postulate that smolt outmigration timing is a key life history trait contributing to variation in the degree of buffering observed within Central Valley Chinook. We believe that critical inter- and intra-population variability in this has been lost due to the large-scale trucking program that releases fish in San Pablo Bay over an unnaturally narrow range of dates and sites. Here we plan to compile and synthesize information on variation in hatchery outplanting strategies both in space (variation among hatcheries) and in time (variation through time for a given hatchery) to quantify whether management practices have homogenized this key life history trait. We will use this set of outplanting strategies to identify realistic baseline scenarios for the theoretical model described in section 3.2.

Third, correlations among rivers might be generated by ocean conditions and other largescale climate effects that all populations share. We will compare the degree of synchronization at the multi-decadal scale (e.g., different PDO phases) as well as among years (e.g., different ENSO phases). In both cases, we will again calculate correlation coefficients between all pairs of rivers within each focal time period for comparison across temporal scales, along with CV in total stock complex size.

We will also explore emerging techniques such as maximum autocorrelation factor analysis (MAF, Fujiwara 2008) to extract trends from the multivariate time series data set consisting of annual returns for each river. In addition, we can explore mechanisms by assessing which environmental or management factors are most correlated with the various MAFs (common contributors to trends in multiple rivers) to assess what conditions are most important to promoting synchrony among different sets of rivers.

Taken together, the knowledge gained from the work described in this section will provide managers guidance on how they might expect water management decisions, hatchery outplanting decisions, or restoration activities to affect correlations among rivers, the effects of which they can explore using the management and visualization tools described in section 3.1.4.
3.1.3.3 Trends in PE strength During the most recent decade, the total return of fall-run Chinook to the Central Valley has been both the largest (2002, $\mathrm{n}=1,441,476$ ) and smallest (2008, $\mathrm{n}=75,788$ ) on record, suggesting evidence of decreased stability in this stock complex. Such a change would be consistent with documented loss of PE in other systems as they decline (Isaak et al. 2003; Moore et al. 2010). We will examine evidence of changes in the stability of the stock complex across the full fifty year time period by calculating mean correlations between rivers across moving windows of a constant length.
3.1.3.4 Predicting effects of PE on stock complex viability The knowledge gained through the activities described in sections 3.1.3.1-3.1.3.3 will provide a framework for describing current contributors to PE in the system, and the likely effects of ongoing trends and new management actions. To translate an estimate of PE into effects on stock complex viability, we will use an approach similar to Hinrichsen (2009). Specifically, we will use multivariate state space models to perform stochastic projections of populations whose mean and variance in production, along with correlation structure, match that displayed in our data set. We will define quasiextinction using a liberal threshold for total Central Valley
fall-run Chinook run size equal to that which triggered the recent closure, as well as the thresholds proposed by Lindley et al. (2009) and explore the predicted frequency of such collapses based on the high and low ends of our confidence intervals on correlations between rivers. In this way, we can quantify the importance of portfolio effect-induced-buffering on preventing economic collapses of stocks. While absolute statements of extinction risk need to be interpreted with great caution, they have value in comparing the relative risks of different scenarios (Beissinger and Westphal 1998; Brook et al. 2000).

### 3.1.4 Management and Visualization Tools: Water and Ecosystem Management Decision Support System Development

### 3.1.4.1 Visualizing effects of changes in evenness and correlations on strength of

PE Doak et al. (1998) provide equations to calculate the percent reduction in coefficient of variation predicted as a function of the number of stocks pooled together, their mean pairwise correlation, and their evenness. We will provide an interactive spreadsheet that solves these equations to allow managers to investigate the PE benefits of various actions, with predicted changes in evenness and correlation structure informed by the work described in section 3.1.3. We will also provide simulation-based R code ( R Development Core Team 2007) quantifying the PE impacts of changes in the mean abundance, variance, and covariance structure of an arbitrarily specified set of stocks with separate dynamics to visualize the PE impacts of changes in more heterogeneous systems that are not easily represented in tractable analytic formulations.
3.1.4.2 Visualizing effects of PE on stock complex viability We will develop code for the population viability analysis in R (R Development Core Team 2007), ensuring crossplatform compatibility and free access. We will document the code via extensive embedded commenting and set the code up for easily modification of input parameters via a command line interface and/or reading from tab delimited text files easily generated using common spreadsheet software such as Microsoft Excel. This will allow easy comparisons of relative risks under different management scenarios predicted to change run sizes or correlation structure as informed by the ecological knowledge gained in sections 3.1.2-3.1.3.

### 3.2 Modeling: integration of ecosystem dynamics and human dimensions

As described in section 2.1.1, while the proximate cause of the recent CVC collapse was poor ocean conditions, the CVC stock complex lacked the resilience to respond to this environmental stressor due to a combination of hatchery, harvest, and water flow practices reducing life history variation (Lindley et al. 2009). In this section we describe our framework for a dynamically-coupled, human-natural system decision model that integrates changing ocean conditions and water flow with hatchery and fishery policy. The empirical synthesis of existing time series described in section 3.1 above will guide the structure of, and test the predicted trends from, this model (described in more detail below). Here we outline our novel combined evolutionary-bioeconomic model to inform the coordinated management of native fish under variable conditions. Our goal is to advance the capacity of managers to
balance two key trade-offs, both of which involve a tension between long-run CVC population viability and short-run economic benefits from natural resource use.

The first trade-off is population-level diversity versus biomass: hatchery efforts to augment salmon stocks within a given generation to support a larger short-run harvest can lead to a loss of genetic diversity due to increased straying across subpopulations (Williamson and May 2005). In addition, the practice of trucking smolts from the hatchery to the estuary increases outmigration survivorship (augmentation) but at the cost of greater straying. Thus our framework models the effect of hatchery production and trucking of smolts on short-term harvest as well as the subsequent impact on straying between subpopulations and the resulting loss of diversity among populations.

We conceptualize this loss in terms of less variation in the phenotypic trait of outmigration timing within and across populations. We represent the PE and hence the value of population-level diversity as the capacity of the CVC stock to buffer against environmental stressors, namely variation in environmental conditions. We incorporate two sources of such variation, one natural and one partly anthropogenic. The natural variation we model involves yearly shifts in ocean conditions, which determine food availability for outmigrating smolts and therefore the optimal ocean arrival timing. Because this ideal arrival time will vary across years, there is value in diversity in the phenotypic trait of outmigration time to reduce the likelihood of large swings in population dynamics and fisheries yield.

The second source of environmental variation is motivated by the second key trade-off: maximizing out-of-stream uses of water generates immediate economic benefits but can cause a loss of diversity in CVC (Lindley et al. 2009). Thus the anthropogenic variation we include involves stream flow, and the issue at hand is a loss of variation of flows. This alters selection on outmigration time within and among populations. In the simplified framework below, we incorporate flow variation as a given or exogenous process. We can then examine how CVC management should respond to anthropogenic stressors. Ultimately we intend to extend the choice model beyond harvest and hatchery actions to include decisions to achieve a water management objective that has implications for flow variation and timing. This will allow us to see how flow management (modification of anthropogenic stressors) should respond, in turn, to the needs of the CVC resource.

Below we first describe the ecological, evolutionary, and economic dynamics of the model. Then we describe how we will analyze the model in order to address our central questions.

### 3.2.1 Dynamics of the evolutionary bioeconomic model

In order to capture the essential dynamics of the PE within the simplest (and therefore most tractable) model possible, we focus on the inter- and intra-stock variation in two rivers, where a hatchery is located on one of the rivers. In addition, among all of the life history traits that contribute to biocomplexity, we focus on outmigration time because of its importance to response to changing water flow and ocean conditions as described above. Therefore, we model environmental heterogeneity through changes in optimal outmigration timing as it depends on ocean conditions. Given the significant genetic contribution to phenological traits in salmon (reviewed in Carlson and Seamons 2008), we follow the evolution of outmigration time in the two rivers and hatchery and couple these evolutionary dynamics to the salmon population dynamics.


Figure 2: Outline of the model dynamics. Each circle indicates the population rearing environment $\left(i \in\left\{A, A^{*}, B\right\}\right)$. Text along the circle indicates different life history stages (with a dashed bar at the census point), inner text indicates evolutionary and ecological dynamics, and outer text indicates management-driven dynamics.

Specifically, we model the evolution of outmigration time as a quantitative genetic trait, where we assume that a large number of unlinked loci each contribute additively to the genotype, and both the genotype and environment contribute to the phenotype. Given the resulting continuous distribution of phenotypic values in a population, we follow the dynamics (change over time) of the phenotypic mean and variance as well as salmon population size for the ecological component of the model. We use this approach of allowing for changing variance in time (based on the framework in Cavalli-Sforza and Feldman 1976), which differs from the typical assumption of constant variances (e.g., the Lande (1976) model used in the hatchery-based selection model by Ford (2002)) because of the importance of phenotypic variation and its dynamics to the PE .

The model follows the population, genetic, and phenotypic dynamics that occur between the major stages in a typical salmon life cycle, summarized in Figure 2. Below we describe the dynamics of these steps in a basic model and indicate intended extensions; Boxes 1-2 provide the mathematical details of the basic model. Possible sources for parameterization include the smolt productivity information in Reisenbichler et al. (2004), the hatchery cost information in USRSSAC (1984), the heritability information in Carlson and Seamons (2008), the selection strength information in Araki et al. (2008), the mutation information in Lynch (1988), the oceanic survivorship and returns information in Lindley et al. (2009), and the straying information in CDFG/NMFS (2001) and Quinn (2005). In addition, simulations driven by hatchery management scenarios identified by the data synthesis described in section 3.1.3.2 will test the capacity for the model to predict realistic qualitative trends as compared to the CVC adult returns from the empirical analysis. We will make all code (commented for accessibility) developed for this model publicly available through online appendices or digital archives associated with publication.
3.2.1.1 Reproduction, hatchery selection, and transport In the river with a hatchery, a given number of salmon are randomly selected from returning adult migrants for hatch-
ery rearing as determined by the hatchery management (similar to Araki et al. (2008) and Ford (2002)). Then the spawners in all rivers reproduce with a location-specific production term (number of smolts per individual, collapsing egg production and egg-to-fry survivorship into one term), which is both phenotype- and density-independent in the basic model. Random mating occurs within each environment, offspring inherit their genotype based on their parental genotypes and the genetic variance, and then offspring phenotypes depend on their genotypes and random environmental variance. As with any model, this basic model makes a number of assumptions for simplicity: we ignore phenotype plasticity (e.g., the evolution of an environmental or conditional trigger for outmigration rather than outmigration timing itself), assortative mating (e.g., based on return migration timing), and hatchery-based selection for earlier life histories or other behavioral and phenotypic traits that affect fitness (Heath et al. 2003; Araki et al. 2008; Hutchings and Fraser 2008; Reisenbichler and Rubin 1999). Model extensions that relax individual assumptions can test their influence on our conclusions.

The hatchery incurs two types of costs: production costs and transport costs. The production costs increase linearly with the number of hatchery fish (similar to Costello et al. 1998). The transport costs depend on the point of hatchery fish release, which can occur at any point between the hatchery and the estuary. Increasing the trucking distance also leads to increased survivorship to smolt stage and increased straying rate of returning adults, which results in a trade-off between population size and genetic homogenization effects (CDFG/NMFS 2001).
3.2.1.2 Selection and environmental variation. Two selection events occur in the model: during outmigration and at ocean arrival. The selection and survivorship during outmigration models the influence of river flow and the selection and survivorship at ocean arrival models the influence of changing ocean conditions on the genetic and phenotypic dynamics of outmigration timing as well as population dynamics. Specifically, in both cases, stabilizing selection based on the distribution of outmigration phenotypes in each population occurs and determines population-level survivorship (similar to the approach in Ford 2002).

During outmigration, selection for an optimal outmigration time occurs in the wild populations and differs between locations. This selection helps to drive the variation in outmigration time across different rivers. In addition, changes to both the optimal outmigration time and selection strength (which determines overall survivorship) can model anthropogenic alterations to flow regimes or the influence of climate change on water flow. Specifically, water operations can affect the overall survivorship in this step or strongly select for a specific outmigration time due to simplification of the migratory habitat (Lindley et al. 2009). Furthermore, a shifting optimal outmigration time to earlier phenotypes can represent the expected climate-change-induced shift toward earlier heavy water flows due to more rain and less mountain snow pack in the western United States (Barnett et al. 2008).

Then, at ocean arrival, temporally heterogeneous selection on outmigration timing occurs. This approach reflects the suggestion that the timing of ocean upwelling onset, which is naturally variable in time, strongly influences juvenile salmon survivorship through bottomup food web dynamics (Lindley et al. 2009). For the hatchery fish, outmigration time can either be phenotype-dependent or determined by hatchery management (trucking time),

Box 1. Model dynamics: reproduction and selection. Here and in Box 2 we present the basic model dynamics. In order to derive the population size and quantitative genetic dynamics from the same set of dynamics, we first construct the model in terms of the population density function for each population $i$ (spawned in river $A$, hatchery $A^{*}$, or river $B$ ) at time (year) $t$ with phenotype $f$ and genotype $g$ denoted $n_{i, t}(f, g)$. From this model we can derive the coupled dynamics of the population sizes $N_{i, t}=\iint n_{i, t}(f, g) d f d g$, the mean phenotype $\mu_{f, i, t}=\iint f n_{i, t}(f, g) d f d g / N_{i, t}$, and the phenotypic variance $F_{i, t}=\iint\left(f-\mu_{f, i, t}\right)^{2} n_{i, t}(f, g) d f d g / N_{i, t}$ for each location $i$ at time $t$.

Reproduction. Assuming random mating, the probability of two individuals mating with a given genotype-phenotype combination within a population is the product of the proportion of individuals with each genotype-phenotype combination (encounter probability). Then the offspring genotype depends on the mean parental genotype, the genetic variance, and the amount that mutation increases genetic variance each generation is $\sigma_{M}^{2}$; the offspring phenotype depends on its genotype and the random environmental variation $\sigma_{E}^{2}$. Integrating over all mating combinations, given reproductive output (fry per individual) $R_{i}$ and the return migrant population densities $n_{i, t}$, the fry density function for each population is (following Cavalli-Sforza and Feldman 1976):

$$
\begin{equation*}
n_{i, t}^{\bullet}(f, g)=R_{i} N_{i, t} \frac{\exp \left[-\frac{(f-g)^{2}}{2 \sigma_{E}^{2}}\right]}{\sqrt{2 \pi \sigma_{E}^{2}}} \iiint \int \frac{\exp \left[-\frac{\left(g-\frac{g_{1}+g_{2}}{2}\right)^{2}}{2\left(G_{i, t} / 2+\sigma_{M}^{2}\right)}\right]}{\sqrt{2 \pi\left(G_{i, t} / 2+\sigma_{M}^{2}\right)}} \frac{n_{i, t}\left(f_{1}, g_{1}\right)}{N_{i, t}} \frac{n_{i, t}\left(f_{2}, g_{2}\right)}{N_{i, t}} d f_{1} d g_{1} d f_{2} d g_{2} . \tag{1}
\end{equation*}
$$

Hatchery production and transport. Hatchery production costs $C_{N}$ increase linearly with the selected population size according with price per individual $p^{*}: C_{N}\left(N_{A^{*}, t}\right)=p^{*} N_{A^{*}, t}$. Hatchery transports costs $C_{X}$ increase with release point $X_{t} \in[0,1]$, expressed as a fraction of the distance between the hatchery $\left(X_{t}=0\right)$ and the estuary $\left(X_{t}=1\right)$. Then hatchery production $R_{A^{*}}$ has a fixed component $\bar{R}_{A^{*}}$ (fry production) and a trucking distance-dependent component $K\left(X_{t}\right)$ (fry-to-smolt survivorship) to give $R_{A^{*}, t}=\bar{R}_{A^{*}} K\left(X_{t}\right)$.
Selection. In wild populations $i=A$ and $i=B$, we apply selection for outmigration time with a location-specific optimum timing $\theta_{i, t}^{\bullet}$ and selection strength $\omega_{i, t}^{\bullet}$ to arrive at the smolt population densities (following Ford 2002):

$$
\begin{equation*}
n_{i, t}^{\S}(f, g)=\exp \left[-\frac{\left(f-\theta_{i, t}^{\bullet}\right)^{2}}{2 \omega_{i, t}^{\bullet}}\right] n_{i, t}^{\bullet}(f, g) \text {. } \tag{2}
\end{equation*}
$$

Analogously, we next apply selection for ocean arrival time for the ocean-conditions-dependent optimum timing $\theta_{t}^{\S}$ and selection strength $\omega_{t}^{\S}$ (same for all populations) to arrive at the outmigrant population densities:

$$
\begin{equation*}
n_{i, t}^{\mathbb{T}}(f, g)=\exp \left[-\frac{\left(f-\theta_{t}^{\S}\right)^{2}}{2 \omega_{t}^{\S}}\right] n_{i, t}^{\S}(f, g) \tag{3}
\end{equation*}
$$

depending on model construction (in Box 1 we show the mathematical representation for the phenotype-dependent case).

In order to model the temporal variation in optimal outmigration time, we will consider two approaches. First, we will employ a stylized model that follows optimal outmigration time as a stochastic variable that changes between two possible regimes, with the potential for within-regime noise and multi-year transitions between regimes. This approach will allow exploration of the relative influence of and impact of changes in differences between regimes, the probability of switching between regimes, within-regime noise, and length of transition between regimes. Second, we will use empirical data on ocean conditions (e.g., Wells et al. 2006,2007 ) to determine the model outcome under observed environmental dynamics.

## Box 2. Model dynamics: Ocean survivorship and return migration.

Density-dependent survivorship. Applying Beverton-Holt-style density dependence gives the population density of ocean sub-adults

$$
\begin{equation*}
n_{i, t}^{\prime}(f, g)=\frac{n_{i, t}^{\mathbb{\top}}(f, g)}{1+\alpha \sum_{i \in\left\{A, A^{*}, B\right\}} N_{i, t}^{\boldsymbol{\top}}}, \tag{4}
\end{equation*}
$$

where the strength of density dependence $\alpha$ can be expressed in terms of the carrying capacity $\kappa$ given $\alpha=(R-1) /(R \kappa)$.
Ocean survivorship and harvest. Given an annual natural mortality rate of $M$, the annual ocean survivorship is $S=\exp (-M)$. In addition, in each year $t$ the fishery manager allows the harvest of $Y_{t}$ individuals of salmon (Box 3). After a three-year ocean residency, the spawning escapement (total stock from brood year $t-3$ available for return to spawning in year $t$ ) for each population is

$$
\begin{equation*}
n_{i, t}^{\dagger}(f, g)=S^{3} n_{i, t-3}^{\prime}(f, g)-\frac{n_{i, t-3}^{\prime}(f, g)}{\sum_{i \in\left(A, A^{*}, B\right)} N_{i, t-3}^{\prime}}\left(S^{2} Y_{t-2}+S Y_{t-1}\right) \tag{5}
\end{equation*}
$$

Return, straying, and hatchery selection. Given the trucking-location $\left(X_{t}\right)$-dependent straying probability of hatchery fish $Q\left(X_{t}\right)$, the probability of hatchery fish returning to river $A$ is $q_{A}\left(X_{t}\right)=$ $1-Q\left(X_{t}\right)$ and to river $B$ is $q_{B}\left(X_{t}\right)=Q\left(X_{t}\right)$. Then the population densities of return migrants to each location are:

$$
\begin{equation*}
n_{i, t}^{\ddagger}(f, g)=n_{i, t}^{\dagger}(f, g)+q_{i}\left(X_{t}\right) n_{A^{*}, t}^{\dagger}(f, g) . \tag{6}
\end{equation*}
$$

Assuming $N_{A^{*}, t}$ individuals are randomly selected for the hatchery from the population in location $A$, the spawners in each population have the densities

$$
\begin{equation*}
n_{A, t}(f, g)=\frac{N_{A, t}^{\ddagger}-N_{A^{*}, t}}{N_{A, t}^{\ddagger}} n_{A, t}^{\ddagger}(f, g) \quad n_{A^{*}, t}(f, g)=\frac{N_{A^{*}, t}}{N_{A, t}^{\ddagger}} n_{A, t}^{\ddagger}(f, g) \quad n_{B, t}(f, g)=n_{B, t}^{\ddagger}(f, g) . \tag{7}
\end{equation*}
$$

3.2.1.3 Density-dependent survivorship. After experiencing selection on outmigration time, the outmigrants undergo density-dependent survivorship using a Beverton-Holt function. In the basic model, all individuals affect each other equally through this densitydependence, regardless of phenotype and spawning location, under the assumption that density dependence occurs over a longer period than the variability in outmigration time among and within populations. While density-dependent mortality can occur at multiple stages in salmon life cycles (e.g., the fry-to-smolt stage; Bjorkstedt 2000), we implement density dependence at this stage given its importance to hatchery-wild fish interactions (Levin et al. 2001) and the central role of mortality at this stage in the recent CVC collapse (Lindley et al. 2009). Specifically, incorporating density dependence at the outmigration stage provides the flexibility to explore the potentially critical role of fluctuations in the amount of ocean productivity (e.g., model poor ocean conditions in terms of lower total productivity as well as any mismatch in timing of outmigration and peak productivity modeled by the selection described in section 3.2.1.2). In addition to a more realistic representation of the temporal heterogeneity that CVC experience, this will account for the effects of hatcheries on wild fish through density-dependent interactions, which can be especially important in years with poor ocean conditions (Levin et al. 2001).
3.2.1.4 Ocean survivorship and harvest. Individuals experience annual harvest as well as natural density-independent mortality. The basic model assumes that these processes are phenotype-independent. For the harvest mortality, we assume that the popu-
lations intermingle and cannot be distinguished by the fishery manager (i.e., we ignore a hatchery-targeted fishery, which is not currently feasible for the CVC). In addition, in the basic model, all surviving salmon return at age three. We will generalize the model to incorporate the potential for individuals to return at different ages, leading to overlapping generations. This component will be of particular interest given its potential importance to population genetics (Waples 2002), the influence of temporally heterogeneous selection on genetic variation (Ellner and Hairston 1994), and the importance of life history diversity in providing further buffering beyond that produced by independent dynamics (Greene et al. 2010).
3.2.1.5 Return and straying. As the surviving ocean adults return to spawn, straying occurs: the proportion of hatchery fish that return to the hatchery-origin river as opposed to the other modeled river depends on the original trucking distance from the hatchery to the release point (CDFG/NMFS 2001). While the basic model focuses on straying in the hatchery population based on the far greater straying rates for trucked hatchery fish than naturally-spawned fish (ca. $80 \%$ vs. 1-5\%; CDFG/NMFS 2001 and Quinn 2005, respectively), we will test the effect of including natural straying on the model predictions. In addition, we will consider the effect of lower spawning migration and/or ocean survival of hatchery-reared fish compared to naturally-spawned fish in order to model unintended fitness consequences of hatchery production (Naish et al. 2007).

### 3.2.2 Modeling insight into the role of population-level diversity and anthropogenic disruption of the PE

> Objective 2: Explore central questions 1 and 2 from a theoretical perspective, determining:
> (a) the influence of withinand between-population diversity in outmigration timing on response capacity to environmental stressors, and
> (b) the consequences of management choices on variation in traits important in generating PEs and on the human systems that exploit those stocks.

To compare the role of different types of population-level diversity in the PE given environmental heterogeneity, we will explore predicted model outcomes given different initial conditions for within- and between-river phenotypic diversity in outmigration time. We will compare how different hatchery, water flow and fishery management approaches affect the natural system in terms of within- and between-river phenotypic variability and the population size mean and variance in time. We will assess subsequent effects on the degree of buffering and potential risk for crossing viability thresholds given variable ocean conditions and river flows, building on the approach in Lindley et al. (2007), and further explore the suitability of the PE metrics described in section 3.1.1 above. In addition, simulations driven by hatchery management scenarios identified by the data synthesis described in section 3.1.3.2 will test the capacity for the model to predict realistic qualitative trends as compared to the CVC adult returns from the empirical analysis.

As stated above, a broad thematic goal of our study will be characterizing the tradeoff between resource use (water and fisheries) or augmentation (hatcheries) and population
homogenization, which can increase the temporal variance of the population size and decrease the stability of the stock complex. We will examine the resource management problem under imperfect information where run size estimates and hence management actions are subject to error (in part due to greater variability), compounding the effect of more volatile population dynamics. It is clear that resource managers are faced with complex dynamics, multiple long-run trade-offs and significant implications for human welfare. For instance, it might be the case that an emphasis on augmentation provides for stronger populations and greater harvest in the short-run but at the expense of long-run viability or variability. How are managers to identify a desirable balance between long-run anticipated benefits of enhancing phenotypic diversity and the potential sacrifices (e.g. to harvest levels) in the short-run? To make well-reasoned decisions which balance ecological trade-offs and are sensitive to social impacts, it is important to specify a clear set of objectives, a problem we turn to in the next section.

### 3.3 Adaptive management for achieving socio-ecological objectives and coordinating institutions

Our analysis will focus on two core issues: the appropriate form of the management objective and the characterization of gains from coordination between agencies governing water, hatcheries, and harvest. Below we outline models for two perspectives on specifying the management objective, alternatively from an economic and a conservation-based standpoint. We describe how these potentially competing objectives can be reconciled in a sustainability framework. We then discuss the second core issue of management coordination across natural resources and how we will examine what opportunities are lost if barriers to coordination are not overcome in our model system.

### 3.3.1 Management objectives: Social welfare and population viability

The first objective is a common formulation stemming from an economic approach: maximize social welfare, defined as the present value of the annual stream of expected benefits from resource harvest net of costs (harvest and augmentation) over a long time horizon. The specifics of the welfare objective are outlined in Box 3. In essence the problem involves choosing levels of resource harvest and augmentation (hatchery production and trucking) to maximize expected discounted net benefits, subject to the model dynamics described in section 3.2. A conservation-based perspective motivates an alternative objective: minimize the probability that the population falls below a minimum viable population size threshold over a specified time frame (e.g. NOAA 2000; Newbold and Siikamaki 2009). Under this formulation, the task is to make choices over resource harvest and augmentation to minimize extinction risk, given the population and phenotypic dynamics described in section 3.2.

While it is not possible to fully optimize over multiple objectives simultaneously, we will consider forms of the problem in which the decision-maker attends to one objective given a constraint on others. This is consistent with a sustainability perspective which emphasizes social welfare needs conditional on the perpetual maintenance of the resource. For example, one approach to reconciling the social welfare and conservation objectives (which might be competing or complementary depending on the setting) is to either (1)
maximize social welfare subject to a maximum acceptable expected likelihood of falling below the viability threshold, or (2) minimize this expected probability subject to a minimum acceptable expected social welfare level. Overall, generating insight into the impacts of the PE on both economic and conservation objectives will inform conservation policy decisions that balance population viability and harvest objectives.

### 3.3.2 Institutional coordination

| Objective 3: | Explore |
| :--- | ---: |
| central question | 3 |
| by eval- |  |
| uating the institutional |  |
| and regulatory feasibility |  |
| of management options |  |
| designed to maintain or |  |
| rebuild the PE. |  |

The type of natural resource we are concerned with (i.e., salmon) features a life history spanning multiple spatial scales and is sensitive to variability in environmental conditions. Therefore, we will examine issues of management coordination across scales and the ability to adapt or adjust policy to change. In the simplified management problems formulated above, resource use (water and fisheries harvest) and resource augmentation (hatchery) actions are chosen jointly by a sole decision-maker. This is a standard representation of the bioeconomic problem (e.g. Costello et al. 1998) from a benevolent social planner perspective.

In reality, however, these resource management decisions are typically made by separate institutions (Molony et al. 2003). In the case of CVC, harvest policy is determined by the Pacific Fisheries Management Council (PFMC) with oversight from NMFS, while augmentation decisions are made by a number of individual state and federally run hatcheries within the system. Further, water diversions are the province of the state Department of Water Resources and the federal Bureau of Reclamation, and all must respond, to some extent, to the conservation judgments of NMFS and the California Department of Fish and Game with respect to threatened or endangered fish. Our research will examine the implicit limitations on managing for adaptive capacity that are imposed when management decisions are made independently, as well as addressing the potential benefits of separating some management functions, and asking whether the existing network of opportunities for coordination is effective.

Analysis of the non-coordinated management setting requires formulating distinct objectives for the water, hatcheries, and fishery management. For the fishery, the standard

Box 3. Economic welfare objective: For simplicity, we include only the benefits from the commercial fishery, setting aside non-use and recreation values for the time being. Following Costello et al. (1998) we characterize net benefits from the fishery as follows. Letting $p$ represent a fixed price per pound and $w$ the average weight per salmon, revenue is given by $Y_{t} \cdot p \cdot w$. In salmon fisheries, variable costs are commonly modeled as a proportion $\gamma$ of revenue. Net benefits or profits from harvesting are given by $\pi\left(Y_{t}\right)=(1-\gamma) \cdot Y_{t} \cdot p \cdot w$. Inclusive of hatchery actions, the net benefits from period $t$, given the choice vector $\mathbf{u}_{\mathbf{t}}=\left\{Y_{t}, N_{A, t}^{*}, X_{t}\right\}$ characterizing decisions over harvest, hatchery production and trucking distance are:

$$
\begin{equation*}
\mathrm{NB}\left(\mathbf{u}_{\mathbf{t}}\right)=\pi\left(Y_{t}\right)-C_{N}\left(N_{A, t}^{*}\right)-C_{X}\left(X_{t}\right) . \tag{8}
\end{equation*}
$$

The social welfare decision problem is to choose a vector of controls $\mathbf{u}_{\mathbf{t}}$ to maximize the expected value of the discounted net benefits over a planning horizon of $T$ years, subject to the population dynamics and environmental variability described above.
approach is to maximize the present value of the annual stream of expected net benefits (profits) from harvest. While contemporary hatchery operations might have specific production goals, they often lack clearly delineated and measurable overarching objectives, either in economic or ecological terms. We will compare multiple specifications of the hatchery objective, including (1) maximize the population of hatchery reared fish available for harvest given a fixed budget constraint, and (2) minimize the cost of providing a target expected number of hatchery reared fish for harvest. Under the non-coordinated hatchery objective, the long-run implications of hatchery decisions are ignored - an incentive to account for the long-term population and genetic effects of augmentation is absent. When we extend the model to incorporate the water management objective we will consider the implications of the major relevant sources of water use: (1) power generation - which incentivizes uniform flow; (2) agricultural use - which incentivizes storage to meet peak growing season demand; and (3) urban use - which incentivizes storage to meet peak summer demand. Our research will include an analysis of cooperative versus fragmented decision-making for resource management, examining the implications of facilitating coordination for social welfare and conservation goals (e.g., the maintenance or restoration of the PE in CVC salmon).

## 4 Feasibility

Feasibility of the synthesis of existing time series depends on the expertise of PI Carlson, co-PI Satterthwaite, and input from co-PI Lindley. All three have extensive experience extracting demographic information from time series data and working with salmonids, and the preliminary results presented in Carlson and Satterthwaite (in review) and section 3.1.2 demonstrate that adequate information is available to quantify the portfolio effect in CVC and its contributing factors.

Feasibility of the evolutionary bioeconomic decision model component of the project depends on the expertise of co-PIs Baskett, Springborn, and Waples and on computational software, which is readily available. Baskett and Waples provide the population genetic modeling expertise while Springborn provides the economic expertise in stochastic dynamic modeling. While the mathematics in Boxes 1-3 is complex, its structure allows simplification to follow the phenotypic mean and variance, rather than entire joint phenotype-genotypic distribution, under the assumption of normality using the analytic approaches in (Cavalli-Sforza and Feldman 1976). In addition, numerical analysis without the assumption of normality is readily feasible with the computational tools developed by Turelli and Barton (1994).

Baskett, Carlson, Lindley Springborn, and Waples are all providing a cost-share of salary and benefits (totaling $\$ 121,367$ ) for part of the time they will spend on the project; these funds are readily available from their respective employers.

## 5 Relevance to the Delta Science Program

### 5.1 Relevance to this PSP

Our proposal directly addresses Topic 1 with a focus on native fish biology and ecology, specifically the protection and recovery of Central Valley fall-run Chinook salmon (CVC).

Our conceptual and numerical modeling will explicitly examine biocomplexity within this stock complex as a component of its long-term resilience. With our evaluation of phenotypic diversity and consideration of evolutionary dynamics, our central focus is on understanding how natural and anthropogenic factors, especially water flow, hatcheries, and fisheries, affect the adaptive capacity of Central Valley Chinook in the face of changing river and ocean conditions. In addition, our primary goal is to provide information on how various management actions are likely to impact or restore portfolio effects in CVC and therefore the prospect for long-term persistence and stability. To this end, we also propose to develop a framework to support management decisions over multiple salmon stocks.

Therefore, our empirical and modeling efforts will also contribute to Topic 4 by informing decision support for water and ecosystem management. First, we will make available code for the open-source program R as well as an interactive Microsoft Excel spreadsheet that will allow managers to visualize the effects of changes in evenness and correlations among stocks on the strength of the portfolio effect in CVC salmon. We will then develop code for a population viability analysis that will allow easy comparisons of relative risks under different management scenarios that are predicted to change run sizes or correlation structure as informed by the ecological knowledge gained through our analyses of existing datasets.

Second, our evolutionary bioeconomic decision model will provide insight for managers and policy-makers into how to balance the trade-offs and interdependencies between managing CVC salmon populations and water flow. Specifically, we develop a model of CVC salmon population dynamics that incorporates the role of both water flow and hatchery management decisions in either homogenizing populations or supporting diversity for a portfolio effect to buffer the effect of environmental change. This approach will improve managers' capacity to balance stocks of biomass, biodiversity, and water resources given variability in climatic conditions. Through this dynamically coupled evolutionary-ecological-economic model, our interdisciplinary team will combine natural and social science to encompass crucial connections in our socio-ecological system and develop support tools for decisions with complex human and biological implications. We will make this decision-support framework readily accessible and available to managers through publication of original code for all modeling components.

### 5.2 Relevance to Delta Science Program Issues Outside this PSP

The focus on management for long-term resilience motivates including biological diversity specifically the genetic and phenotypic diversity in CVC salmon - as a key stock variable, in combination with the traditional focus on fish biomass and water resources. Such an understanding of diversity within species is critical to the ecosystem-based management (EBM) goal of promoting long-term sustainability of resource use, but it has tended to receive less attention in EBM than the role of diversity among, and interactions between, species (Schindler et al. 2010). Through our focus on the portfolio effect, our work will contribute to efforts to structurally incorporate biodiversity on multiple ecological scales (within and across populations) in resource management. Therefore, this project will provide a unique contribution to EBM within the California Bay-Delta system and beyond.

## 6 Qualifications

This collaboration builds on the complementing expertise of a balanced multidisciplinary research team. The team encompasses empirical expertise in salmonid systems (Carlson, Lindley, Satterthwaite, Waples), anthropogenic selection (Carlson), linkages between the physical environment and ecological dynamics (Lindley), stochastic demography (Lindley, Satterthwaite), diversity and genetics of spatially structured populations (Waples), theoretical expertise in conservation genetics (Waples), coupling evolutionary and ecological dynamics in human-dominated systems (Carlson, Baskett), life history theory (Satterthwaite), and economic expertise in dynamic stochastic management models (Springborn). The UC Berkeley GSR, under the guidance of Carlson and Satterthwaite, will assist with synthesizing existing data sets, time series modeling, and disseminating results. The UC Davis GSR, under the guidance of Springborn and Baskett, will assist with analysis and dissemination of the bioeconomic model, including specification, parameterization, scenario-building, simulation of scenarios and model optimization. Lead PI Carlson will be responsible for project management and administrative activities. Carlson, Satterthwaite, Lindley, and Berkeley GSR will perform all empirical analyses, with guidance from all other PIs. Springborn, Baskett, Waples, and UC Davis GSR will construct the evolutionary bioeconomic model, with guidance from all other PIs.

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June 30, 2010

## Delta Science Program

2010 Proposal Solicitation Package
$F X+19164457311$
Subject: $\quad$ Proposal Number: 2010.01-0112
UCB Proposal Number: 20103867
Project Title: Managing natural resources for adaptive capacity: the Central Valley Chinook salmon portfolio
UCB Principal Investigator: Stephanie Carlson
Period of Performance: 07/01/2011-06/30/2014
Amount Requested: $\$ 489,343$

## To Whom It May Concern:

The University of California Berkeley is pleased to submit the signature page on behalf of the Regents of the University of California. The submission of these documents demonstrates our commitment to the proposed research. The University representative to whom questions may be directed and with whom award negotiations may be conducted is Deborah Rutkowski-Howard, who may be reached at deborahr@berkeley.edu or at (510) 643-5603.

Please note: We want to point out some issues we have with the sample agreement. If selected for funding, we will have to negotiate the following terms and conditions:

## Attachment | General Terms and Conditions for Delta Science Program Grants

I) Item 5-Indemnification: We request mutual indemnification.
2) Item 7 - Termination for Cause: We cannot accept this clause as is. As a non-profit, academic institution we do not have the resources to accept any financial liability.
3) Item 12 - Travel: We request the ability to use UC travel rates as allowed in the State Control Manual Section 3.18.
4) Item 16 - Withholding of Grant Disbursement: As a non-profit, academic institution, we operate on an at-cost basis. All allowable expenses in accordance with the scope of work should be paid irrespective of any disputes.

## Attachment | Special Terms and Conditions for Delta Science Program Grants

5) Item 11 -Rights in Data: We would prefer to have this clause tightened. The word "produced" should be replaced with the word "delivered".

Should this proposal be selected for funding, please issue contract documents and attachments suitable to a non-profit, educational institution in the University's corporate name to the following address:

The Regents of the University of California
coo Sponsored Projects Office
2150 Shattuck Ave., Suite 313
Berkeley, CA 94704-5940
Email: spoawards@berkeley.edu
Thank you for your consideration of this proposal,


Associate Director

## Delta Science Program 2010 Proposal Solicitation Package

## 2010 PGP SIGNATURE PAGE

The applicant for this proposal must submit the signature form by printing it, having it signed, scanning the signed form, and uploading the scanned document by using the "upload" button on the signature page form on our website. If you do not have access to a scanner, you may submit your signed form via FAX to (916) 445-7311. Please send only one form per FAX transmission.

Failure to sign and submit this form, by the submission deadline, will result in the application not being considered for funding. The Primary Contact for this proposal will receive e-mail confirmation as soon as this signature page has been processed.

By signing below, I declare that:

- All representations in this proposal are truthful;
- I am authorized to submit the application on behalf of applicant (if applicant is an entity or organization);
- I have read and understand the conflict of interest section in the main body of the PSP and waive any and all rights to privacy and confidentiality of the proposal on behalf of the applicant, to the extent provided in this PSP, and
- I have read and understood all attachments of this PSP.

Proposal Title:
Lead Investigator:
Organization:
Proposal \#:

Managing natural resources for adaptive capacity: the Central
Valley Chinook salmon portfolio
Stephanie Carlson
Berkeley, California University of
2010.01-0112

Signatory for the applicant organization:

(Please print the name of the signatory)


Signature


Date

## Salutation Dr.

Last Name Carlson
First Name Stephanie
Title Assistant Professor of Freshwater Fish Ecology
Organization University of California, Berkeley
Position lead PI
Email: smcarlson@berkeley.edu

## Qualifications

PI Carlson brings expertise in evolutionary ecology of Pacific salmon to the project (e.g., Carlson and Quinn 2007, Carlson and Seamons 2008, McClure et al. 2008, Carlson et al. 2009). The project builds directly on her research program to understand the causes and consequences of diversity among salmon populations (e.g., Carlson and Satterthwaite In Review), and to apply evolutionary principles to guide conservation, management, and restoration efforts. The project also builds on her recent efforts to understand how anthropogenic selection affects wild populations (e.g., Carlson et al. 2007, Edeline et al. 2007, Darimont et al. 2009). Carlson has substantial experience synthesizing, managing, and analyzing large, empirical data sets (e.g., Carlson and Seamons 2007, Siepielski et al. 2009). Her emphasis will be on project management, contributing to all phases of the empirical analyses, and providing guidance on the evolutionary bioeconomic model.

## Relevant publications

Carlson, S.M., and Satterthwaite, W.H. In Review. Weak portfolio effect in a collapsed fish population complex. Proceedings of the Royal Society B.
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## Salutation Dr.

Last Name Springborn
First Name Michael
Title Assistant Professor in Ecosystem Service Valuation
Organization University of California, Davis
Position Co-PI
Email: mspringborn@ucdavis.edu

## Qualifications

PI Springborn brings to the project extensive experience with multi-state, multi-decision (control) variable optimization problems under uncertainty in a stochastic dynamic programming framework (Springborn et al. 2010, Fischer and Springborn In Revision). He also has experience with integrated ecological and bioeconomic modeling of both fisheries and habitat (Sanchirico and Springborn In Revision). Springborn has experience working with natural and social science interdisciplinary teams on environmental policy problems (Working group on "Effects of trade policy on management of non-native forest pests and pathogens" supported by National Center for Ecological Analysis and Synthesis (NCEAS) (2008-2010); Working group on "Synthesizing and Predicting Infectious Disease while accounting for Endogenous Risk (SPIDER)" supported by the National Institute for Mathematical and Biological Synthesis (NIMBioS) (2009-2010); UC Davis Agricultural Sustainability Institute, working group on "Nitrogen science, climate change and agriculture" (2009-2010)).

## Relevant publications

Sanchirico, J.N., and Springborn, M. In Revision. How to get there from here: Ecological and economic dynamics of ecosystem service provision.
Fischer, C., and Springborn, M. In Revision. Emissions targets and the real business cycle: Intensity targets versus caps or taxes.
Springborn, M., Costello, C.J., and Ferrier, P. In Press. Optimal random exploration for trade-related non-indigenous species risk. In "Bioinvasions and Globalization: Ecology, Economics, Management, and Policy", eds. C. Perrings, H. Mooney, and M. Williamson. Oxford University Press, Oxford.

Springborn, M., Costello, C.J., and McAusland, C. June 2008. Policy and risk processes of trade-related biological invasions. U.S. Department of Agriculture, Economics Research Report.
Costello, C.J., Springborn, M., McAusland, C., and Solow, A. 2007. Unintended biological invasions: Does risk vary by trading partner? Journal of Environmental Economics and Management 54: 262-276.

## Salutation Dr.

Last Name Baskett
First Name Marissa
Title Assistant Professor in Quantitative Animal Conservation Ecology
Organization University of California, Davis
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## Qualifications

PI Baskett brings ecological and evolutionary modeling expertise to the project. The project directly builds on her research program of modeling anthropogenically-driven rapid evolutionary change to investigate basic science questions about the interaction between ecological and evolutionary dynamics while informing management. She has substantial experience in building and analyzing quantitative genetic models similar to the one proposed here, with previous applications spanning from fisheries-based to climate change-driven selection (e.g., Baskett et al. 2005, 2009, 2010).

## Relevant publications

Baskett, M.L., Nisbet, R.M., Kappel, C.V., Mumby, P.J., and Gaines, S.D. 2010. Conservation management approaches to protecting the capacity for corals to respond to climate change: a theoretical comparison. Global Change Biology 16: 1229-1246.
Baskett, M.L., Gaines, S.D., and Nisbet, R.M. 2009. Symbiont diversity may help coral reefs survive moderate climate change. Ecological Applications 19: 3-17.
Dunlop, E.S., Baskett, M.L., Heino, M., and Dieckmann, U. 2009. The propensity of marine reserves to reduce the evolutionary effects of fishing in a migratory species. Evolutionary Applications 2: 371-393.
Baskett, M.L., and Halpern, B.S. 2009. Marine Ecosystem Services. In "Guide to Ecology", ed. S.A. Levin. Princeton University Press, Princeton, NJ.
Baskett, M.L., Weitz, J.S., and Levin, S.A. 2007. The evolution of dispersal in reserve networks. American Naturalist 170: 5978.
Baskett, M.L. 2007. Simple fisheries and marine reserve models of interacting species: an overview and example with facilitation. CalCOFI Reports 48: 71-81.
Baskett, M.L., Micheli, F., and Levin, S.A. 2007. Designing marine reserves for interacting species: Insights from theory. Biological Conservation 137: 163-179.
Baskett, M.L. 2006. Prey size refugia and trophic cascades in marine reserves. Marine Ecology Progress Series 328: 285-293.
Baskett, M.L., Yoklavich, M., and Love, M.S. 2006. Predation, competition, and the recovery of overexploited fish stocks in marine reserves. Canadian Journal of Fisheries and Aquatic Sciences 63: 1214-1229.
Baskett, M.L., Levin, S.A., Gaines, S.D., and Dushoff, J. 2005. Marine reserve design and the evolution of size at maturation in harvested fish. Ecological Applications 15: 882-901.

## Salutation Dr.

Last Name Satterthwaite
First Name William
Title Assistant Research Applied Mathematician
Organization University of California, Santa Cruz
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## Qualifications

PI Satterthwaite brings expertise in demographic analyses and salmonid life histories. The project directly builds on his research program of demographic and life history analyses of the strategies organisms use to cope with a varying environment. He has substantial experience in basic and applied analyses of demographic data (Satterthwaite et al. 2002, Satterthwaite et al. 2007, Finkelstein et al. 2008) and responses to the environment at the individual- through population-level. He has worked on unified theoretical and empirical investigations of California salmonids and their Central Valley habitats (e.g., Carlson and Satterthwaite In Review), including a recent 3-year CALFED funded study on life history decisions in juvenile steelhead (Beakes et al. in press, Mangel and Satterthwaite 2008, Satterthwaite et al. 2009, Satterthwaite et al. 2010, Simon et al. in review).

## Relevant publications

Carlson, S.M., and Satterthwaite, W.H. In Review. Weak portfolio effect in a collapsed fish population complex. Proceedings of the Royal Society B.
Simon, C., Satterthwaite, W.H., Beakes, M.P., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., and Mangel, M. In Review. Individual and population level variation in growth parameters for steelhead trout Oncorhynchus mykiss in central California. Transactions of the American Fisheries Society.
Beakes, M. P., Satterthwaite, W.H., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., and Mangel, M. In Press. Smolt transformation in two California populations of steelhead: effects of temporal variability in growth. Transactions of the American Fisheries Society.
Satterthwaite, W.H., Beakes, M.P., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., and Mangel, M. 2010. State-dependent life history models in a changing (and regulated) environment: Steelhead in the California Central Valley. Evolutionary Applications 3: 221-243.
Satterthwaite, W.H., Beakes, M.P., Collins, E.M., Swank, D.R., Merz, J.E., Titus, R.G., Sogard, S.M., and Mangel, M. 2009. Steelhead life history on California's central coast: insights from a state dependent model. Transactions of the American Fisheries Society 138: 532-548.
Mangel, M., and Satterthwaite, W.H. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. Bulletin of Marine Science 83: 107-130.
Finkelstein, M., Bakker, V., Doak, D.F., Sullivan, B., Satterthwaite, W.H., Lewison, R., McIntyre, P.B., Wolf, S., Priddel, D., Arnold, J.M., Henry, R.W., Sievert, P., and

Croxall, J. 2008. Evaluating the potential effectiveness of compensatory mitigation strategies for marine bycatch. PLoS One 3: e2480 doi:10.1371/journal.pone.0002480.
Satterthwaite, W.H., Holl, K.D., Hayes, G.F., and Barber, A.L. 2007. Seed banks in plant conservation: case study of Santa Cruz tarplant restoration. Biological Conservation 135: 57-66.
Satterthwaite, W.H., Menges, E.S., and Quintana-Ascencio, P.F. 2002. Assessing scrub buckwheat population viability in relation to fire using multiple modeling techniques. Ecological Applications 12: 1672-1687.
Harding, E.K., Crone, E.E., Elderd, B.D., Hoekstra, J.M., McKerrow, A.J., Perrine, J.D., Regetz, J., Rissler, L.J., Stanley, A.G., Walters, E.L., and NCEAS Habitat Conservation Plan Working Group. 2001. The scientific foundations of habitat conservation plans: a quantitative assessment. Conservation Biology 15: 488-500.

## Salutation Dr.

Last Name Lindley
First Name Steven
Title Ecologist, Landscape Ecology Team Leader
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## Qualifications

PI Lindley has expertise modeling population dynamics and time series analysis, including application of state-space techniques. He is also an expert in the ecology of Central Valley Chinook salmon, and has led technical teams evaluating their status, prescribing criteria for population performance, and investigating the causes of the recent collapse of the fall-run Chinook fishery.

## Relevant publications/reports

Lindley, S.T., Grimes, C.B., Mohr, M.S., Peterson, W., Stein, J., Anderson, J., Bottom, D., Botsford, L., Busack, C., Collier, T., Ferguson, J., Grover, A., Hankin, D., Kope, R., Lawson, P., Low, A., MacFarlane, B., Moore, K., Palmer-Zwahlen, M., Schwing, F., Smith, J., Tracy, C., Webb, R., Wells, B., and Williams, T. H. 2009. What caused the Sacramento River fall Chinook salmon stock collapse? NOAA Tech Memo NMFS-SWFSC 447.
Mora, E.A., Lindley, S.T., Erickson, D.L., and Klimley, A.P. 2009. Do impassable dams and flow regulation constrain the distribution of green sturgeon in the Sacramento River, California? Journal of Applied Ichthyology 25(S2): 39-47.
Heublein, J.C., Kelly, J.T., Crocker, C.E., Klimley, A.P., and Lindley, S.T. 2009. Migration of green sturgeon, Acipenser medirostris, in the Sacramento River. Environmental Biology of Fishes 84: 245-258.
Rundio, D.E., and Lindley, S.T. 2008. Seasonal patterns of terrestrial and aquatic prey abundance and their use by Oncorhynchus mykiss in a coastal basin with a Mediterranean climate. Transactions of the American Fisheries Society 137: 467480.

Lindley, S.T., Moser, M.L., Erickson, D.F, Belchik, M., Welch, D., Rechiski, E., Kelly, J.T., Heublein, J., and Klimley, A.P. 2008. Marine migration of North American green sturgeon. Transactions of the American Fisheries Society 137: 182-194.
Schick, R.S., and Lindley, S.T. 2007. Directed connectivity among fish populations in a riverine network. Journal of Applied Ecology 44: 1116-1126.
Lindley, S.T., Mora, E., Schick, R.S., Adams, P.B., Anderson, J.J., Greene, S., Hanson, C., May, B.P., McEwan, D., MacFarlane, R.B., Swanson, C., and Williams, J.G. 2007. Framework for assessing viability of Chinook salmon and steelhead in the Sacramento-San Joaquin basin. San Francisco Estuary and Watershed Science 5: Article 4.
Newman, K.B., and Lindley, S.T. 2006. Accounting for demographic and environmental stochasticity, observation error and parameter uncertainty in fish population dynamics models. North American Journal of Fisheries Management 26: 685-701.

Newman, K.B., Buckland, S.T., Lindley, S.T., Thomas, L., and Fernandez, C. 2006. Hidden process models for animal population dynamics. Ecological Applications 16: 74-86.
Lindley, S.T. 2003. Estimation of population growth and extinction parameters from noisy data. Ecological Applications 13: 806-813.
Lindley, S.T., and Mohr, M.S. 2003. Modeling the effect of striped bass (Morone saxatilis) on the population viability of Sacramento River winter-run Chinook salmon (Oncorhynchus tshawytscha). Fishery Bulletin (U.S.) 101: 321-331.

## Salutation Dr.

Last Name Waples
First Name Robin
Title Senior Scientist
Organization National Marine Fisheries Service
Position Co-PI
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## Qualifications

PI Waples has considerable experience in building models to gain insights into dynamic processes in natural populations. He modified standard population genetic models to account for the unusual life history traits of Pacific salmon (Waples 1990), and these models have been widely used for estimating key parameters such as effective population size and the rate of loss of genetic diversity. More recently, models he has helped develop have considered the eco-evolutionary consequences of variability in population growth rate (Waples et al. 2010) and the importance of environmental predictability for phenotypic plasticity (Reed et al. In Press). He has also published widely on effects of salmon hatcheries on natural populations (Waples 1999), as well as the effects of human changes to salmon ecosystems (Gustafson et al. 2007, Williams et al. 2008, Waples et al. 2008). For over a decade, Waples led an interdisciplinary team within NOAA charged with developing the scientific basis for ESA listing determinations and recovery planning for Pacific salmon, and he currently is PI for two different NCEAS projects ("Responses of Pacific salmon to climate change", and "Red flags and species endangerment: Meta-analytical development of criteria for assessing extinction risk").

## Relevant publications

Reed, T.E., Waples, R.S., Schindler, D.E., Hard, J.J., and Kinnison, M.T. In Press. Phenotypic plasticity and population viability: the importance of environmental predictability. Proceedings of the Royal Society of London B.
Waples, R.S. 2010. Spatial-temporal stratifications in natural populations and how they affect understanding and estimation of effective population size. Molecular Ecology Resources (published online May 2010; doi: 10.1111/j.1755-0998.2010.02876.x).
Waples, R.S., Jensen, D.W., and McClure, M.M. 2010. Eco-evolutionary dynamics: Fluctuations in population growth rate reduce effective population size in Chinook salmon. Ecology 91: 902-914.
Waples, R.S., Pess, G.R., and Beechie, T. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evolutionary Applications 1: 189-206.
Williams, J., Zabel, R.W., Waples, R.S., Hutchings, J.A., and Connor, W.P. 2008. Potential for anthropogenic disturbances to influence evolutionary change in the life history of a threatened salmonid. Evolutionary Applications 1: 271-285.
Gustafson, R., Waples, R.S., Myers, J.M., Hard, J.J., Bryant, G.J., Johnson, O.W., and Weitkamp, L.A. 2007. Pacific salmon extinctions: Quantifying lost and remaining diversity. Conservation Biology 21: 1009-1020.

Waples, R.S., and Gaggiotti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Molecular Ecology 15: 1419-1439.
Manel, S., Gaggiotti, O., and Waples, R.S. 2005. Assignment methods: matching biological questions with appropriate techniques. Trends in Ecology and Evolution 20: 136-142.
Waples, R.S., Teel, D.J., Myers, J., and Marshall, A. 2004. Life history divergence in Chinook salmon: Historic contingency and parallel evolution. Evolution 58: 386403.

Waples, R.S. 1999. Dispelling some myths about hatcheries. Fisheries 24: 12-21.
Waples, R.S. 1998. Separating the wheat from the chaff: Patterns of genetic differentiation in high gene flow species. Journal of Heredity 89: 438-450.
Waples, R.S. 1990. Conservation genetics of Pacific salmon. II. Effective population size and the rate of loss of genetic variability. Journal of Heredity 81: 267-276.

