

Disentangling freshwater and marine drivers of salmon populations in the California Current Large Marine Ecosystem and projecting the impacts of climate change

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Background

Salmon constitute an important indicator of ecosystem status for the Integrated Ecosystem Assessment (IEA) of the California Current Large Marine Ecosystem (CCLME, Levin and Schwing 2011). As important members of the food web, in which their success co-varies with those of other species of interest (Roth et al. 2007, Sydeman et al. 2008, Ford et al. 2010), salmon provide direct and indirect reflections of ecosystem health in a broader context. Pacific salmon are also highly valued economically through major commercial fisheries, culturally by Native American tribes, and socially through an enjoyment of nature and a recreational fishery. Nonetheless, many stocks have experienced major declines, earning protection under the Endangered Species Act and stimulating research into what factors regulate salmon abundance. Although strong correlations between ocean environmental drivers and salmon survival have been characterized, much of the variation in salmon population dynamics remains unexplained. Salmon have complex life histories that include spawning, rearing, and migration in the freshwater environment, which contributes to variation in salmon populations. Furthermore, as climate change will likely manifest in different rates of change in the freshwater (FW) and marine (M) environments, understanding the drivers acting across the entire life cycle of salmon in both environments is a high priority for the IEA.

The physical conditions in the ocean that correlate well with marine growth and survival for Chinook (Quinn et al. 2005, Scheuerell and Williams 2005, Zabel et al. 2006, Wells et al. 2008) and coho salmon (Ryding and Skalski 1999, Cole 2000, Hobday and Boehlert 2001, Koslow et al. 2002, Wang et al. 2009) include sea surface temperature (SST) and height, salinity, the Pacific Decadal Oscillation (PDO), upwelling, wind stress or curl, and mixed-layer depth. The state of the ocean also correlates with salmon productivity over the entire life cycle, as measured by recruits-per-spawner (Levin 2003, Mueter et al. 2005, Wang et al. 2009), but it often does not explain a large proportion of the variation in population growth rate. For example, Levin (2003) found that the number of recruits-per-spawner was not significantly associated with the PDO index over extended time periods, partly because the direction of the relationship changed under different ocean regimes. Mueter et al. (2002) found significant correlations with SST, but most correlation coefficients were less than 0.4. Thus, with only ocean drivers, our ability to interpret annual fluctuations and project future population trends is very limited. Several papers have identified FW conditions as being at least as important, if not more important, than ocean conditions in determining population growth rate. For example, Greene et al. (2005) found that ocean conditions explained only 5% of the variation in adult return rates of Skagit River Chinook, compared with riverine and estuarine conditions; Arthaud et al. (2010) found that rearing flow best predicted Lemhi River adult returns. However, no comprehensive comparison within or among Evolutionarily Significant Units (ESUs) of the relative importance of

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environmental drivers among life-history stages exists. We propose to directly evaluate the relative importance of environmental drivers in FW and M environments in explaining variation in population replacement rate among populations across the CCLME and implications of climate change for salmon recovery.

Relating environmental drivers to salmon production presents several challenges. First, many of the drivers within each environment (FW or M) and between the two environments reflect large-scale physical processes, and therefore exhibit multicollinearity. Within the M environment, numerous ocean indices reflect the strength of transport of cool, productive Arctic water into the California Current. Sea surface temperature, sea level height, upwelling intensity, and cool-water copepod abundance are physically linked to some extent. It can thus be difficult to isolate the primary driving force(s). FW drivers can also be physically linked. Furthermore, atmospheric teleconnections, such as El Niño, connect FW and M conditions. Some of the problems associated with within-environment multicollinearity can be handled by a composite index (see Approach), and indices of teleconnections can be tested and included as covariates. However, correlations between FW and M indices make it difficult to determine how different rates of change in the two environments will affect salmon populations. We will approach this problem by thoroughly exploring the correlation structure of environmental drivers, both within and among environments, and clearly identifying the uncertainty of our projections.

A second challenge for identifying FW drivers across many populations is that the particular environmental drivers affecting survival vary by life stage and local habitat characteristics. For example, overwinter flows are critical for egg survival in locations prone to flooding, whereas high temperature in mid-summer often limits stream-dwelling juveniles in warm locations. To solve this problem, we will identify populations in a variety of habitats, incorporate FW drivers at the appropriate spatial and temporal scale, and test appropriate functional forms (e.g., a non-linear response to temperature and flow). Again, we will use well-validated mechanistic hypotheses to set up our alternative hypotheses and collect data either measured or modeled for local conditions.

In summary, marine conditions are important drivers of salmon survival in the ocean, but do not adequately explain variation in population growth rates, which depend partly on freshwater productivity. In populations where FW and M drivers have been compared, FW drivers explained a great deal of the variation in population dynamics. However, this comparison has not been made for the majority of salmon populations in the CCLME. Thus, the following questions remain at the spatial scale of the California Current:

- To what extent are FW and M drivers correlated?
- How much of the variability in salmon productivity do FW and M drivers explain in each environment separately, and over the whole life cycle?
- How will climate-change induced trends in these FW and M drivers affect salmon productivity across the CCLME?

We propose to address these questions with a systematic approach to selecting and evaluating FW and M drivers, a thorough exploration of their correlation structure, and their relative

contribution to freshwater and total salmon productivity. Finally, we will use these results to project population responses to climate-change scenarios.

Approach

To identify freshwater and marine drivers of salmon productivity and project salmon responses to climate-change scenarios, we propose three steps:

Step 1: Assemble a data set of potential FW and M drivers

To the extent possible, we will develop *a priori* criteria that all predictor variables must meet, including 1) clear mechanistic links with survival, 2) appropriate temporal and spatial extents specific to populations with biological data, and 3) data sets that will likely be maintained in the foreseeable future. We will begin with a comprehensive review of potential environmental drivers from the literature, and locate existing environmental data relevant to salmon populations in the CCLME. We will collate monthly streamflow data from the nearest USGS gage (<http://waterdata.usgs.gov/nwis/rt>) and monthly temperature data from local water if possible, otherwise from air measurements (WRCC 2012). We will identify oceanographic data closest to the location of marine entry for each population, following Wells et al. (2008). We will exclude some important factors, such as competition (Wenger et al. 2011), predation (Emmett and Sampson 2007), and disease (Jacobson et al. 2008, Connors et al. 2010), if data are not available for the majority of populations, or existing data sets are too short.

We will then conduct a thorough correlation analysis of all indices, appropriately lagged to match our mechanistic hypotheses. For example, temperature might affect freshwater productivity by increasing pre-spawn mortality during the adult migration year, or by affecting juvenile growth during the first year after hatching, so we will assess the correlation between summer temperature in year t and year $t + 1$. We will use results from this correlation analysis to clarify the mechanisms that can and cannot be distinguished for each population, given the data. For example, summer temperature and summer flow are likely to be highly correlated, and hence statistically indistinguishable, but sequential years might be more independent. FW and M drivers also might be more highly correlated for coastal than inland populations. We will produce a map showing the degree to which we can explore the relative importance between FW and M drivers, and that of individual drivers within each environment, throughout the CCLME.

Where potential drivers are strongly correlated within either the FW or M environment, we will develop composite indices to handle multicollinearity. We will apply appropriate dimension-reduction techniques, such as Principal Components Analysis, or Dynamic Factor Analysis (DFA, Zuur et al. 2003) where strong temporal autocorrelation exists. DFA is specifically designed to extract common patterns in multiple time series. Thus, we will eliminate multicollinearity among environmental factors by using the generated latent trends in further analysis of population responses.

Step 2: Relative importance of the FW and M drivers for population productivity

Our larger goal is to test the utility of FW and M drivers for explaining variation in salmon responses. For the purposes of the IEA, understanding the drivers of FW productivity and M

survival is most useful if it yields insight into changes in population abundance between generations. However, understanding how these drivers affect survival in the two environments separately provides important mechanistic information. Our hypotheses thus span models that require life-stage specific data (and hence can only be tested on relatively few populations that have smolt and adult counts) to those that can be answered with simple spawner counts (and consequently can be tested on a large number of populations).

Our initial hypothesis (H1) is that FW drivers only affect freshwater survival and M drivers only affect marine survival. Thus, given a basic spawner to smolt relationship such as a Beverton-Holt or Ricker function, we would test whether environmental drivers affect the residuals or one of the model parameters (Peterman et al. 2009). We will then test whether marine survival is a function of both M and FW drivers, because of reports that freshwater conditions can affect marine survival (Scheuerell et al. 2009, Petrosky and Schaller 2010, Haeseker et al. 2012). With these populations, we can also compare variability in the freshwater and marine life stages with variability in population growth rate, which might provide insight into whether one or the other set of drivers will dominate the response at the full life-cycle level.

Our second hypothesis (H2) is that both FW and M drivers limit population replacement rate, which we will test in a similar fashion as H1, except that the response variable will be adult recruits-per-spawner (H2.1) rather than smolts-per-spawner. We will test H2.1 on populations with age structure data for returning adults, which is necessary to calculate recruits-per-spawner. We can address this same core question in a broader suite of populations for which we do not have age-structured data, but only escapement and catch (H2.2; at least 81 Chinook and 39 coho) using slightly different statistical techniques. Again, we will compare FW and M drivers of population abundance, but we expect greater temporal autocorrelation because of overlapping cohorts in this response variable. Therefore, we may opt to employ more sophisticated statistical techniques (e.g., multivariate autoregression state-space analysis or MARSS, Holmes et al. 2012). Each of these three response variables has its own set of uncertainties and limitations. We will look for commonalities in the factors across all three approaches, and explain discrepancies when conclusions differ among response variables.

We will analyze each of these response variables using a mixed-effects hierarchical modeling approach (Zuur et al. 2009). The various drivers discussed in Step 1 will enter into a Generalized Linear Mixed Model (GLMM) as fixed-effect covariates. We will group populations either by genetic structure (e.g., Major Population Group or ESU) or habitat characteristics (e.g., rain-versus snow-dominated habitats) and treat population as a random effect within these groups. The GLMM approach also allows us to explore correlated error structures that might reflect temporal or spatial autocorrelation (Zuur et al. 2009). We will use standard model-selection criteria (Akaike Information Criterion) to compare models and identify important FW and M drivers.

Step 3: Projected impacts of climate change

Climate change will dramatically impact the California Current Ecosystem (Bakun 1990, McGowan et al. 1998, Snyder et al. 2003, Hauri et al. 2009, Wang et al. 2010, Stock et al. 2011). Salmon are unique among the IEA indicator species in their sensitivity to both freshwater and marine influences. Salmon performance will likely decline with climate change in both freshwater (Crozier et al. 2008) and marine (Zabel et al. 2006) environments, and availability of

thermally suitable ocean habitat will likely decline (Abdul-Aziz et al. 2011). However, projections of the relative impact of changes in FW and M environments have been hindered by uncertainty in physical projections, such as the intensity and timing of upwelling and decadal oscillations, as well as uncertainty in how salmon will respond behaviorally and physiologically to these changes. Nonetheless, climate change scenarios are being downscaled for the CCLME-IEA based on the Regional Oceanic Modeling System (ROMS) to a resolution sufficient for modeling biological responses (Gruber et al. 2012, personal comm. with IEA team). We will use our models to explore potential salmon responses to these scenarios, combined with freshwater projections (e.g., Climate Impacts Group at the University of Washington; <http://www.hydro.washington.edu/2860/>) from a variety of emissions scenarios, global atmospheric models, and downscaling approaches. In addition to exploring responses to specific scenarios projected over a 20- to 50-year time frame, we will conduct a thorough sensitivity analysis of population responses to systematic declines in the two environments (FW and M) independently and in concert. Through these exercises, we will identify key environmental thresholds that would dramatically increase the risk of extinction of these ESUs, based on pseudo-extinction abundance criteria (e.g., Crozier et al. 2008).

Benefits

Our proposal is unique in providing a coast-wide projection of the combined effects of FW and M climate change on multiple life stages of salmon in the CCLME. This work will contribute to the existing IEA activities by 1) linking drivers and pressures to the salmon indicator of ecosystem condition in a systematic treatment from Washington to California; 2) explicitly assessing FW and M drivers, which differentiate salmon from other indicators of the CCLME; and 3) providing projected impacts of climate change for this important component of the ecosystem. Importantly, we will specifically address a critical need of the IEA. Within the Drivers-Pressures-States-Impacts-Responses framework (DPSIR; Levin et al. 2008), current efforts have focused on the latter portion of SIR (Kurt Fresh, NWFSC, personal communication). Our proposed work focuses on the former portion of DPS to determine how Drivers and Pressures relate to States. Here, we define climate change as a Pressure, which will influence the relationship between Drivers (FW and M drivers) and States (salmon abundance). Our projected climate-change responses will inform risk analyses by identifying biologically relevant reference points with thresholds related to environmental change that present particular risks for population recovery. Results from this effort can be incorporated into the IEA (Phil Levin, personal communication) and serve as an example of connecting the DPSIR framework from Drivers through Responses. We will work closely with members of the IEA team including Phil Levin (NWFSC) and Brian Wells (SWFSC).

Deliverables

We will produce a technical report to provide background information, a thorough literature review, a detailed methodology, a list of the key environmental drivers of salmon population growth, and projected states of salmon indicators in various climate change scenarios to aid in the interpretation of trends discussed in the IEA for the CCLME. We will present our findings at the FATE annual meeting and another professional meeting, and publish at least one peer-reviewed paper.

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