1. Title: **A meta-analysis of climate-driven changes in vital rates**

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4. Associated NMFS Fisheries Science Center:	Southwest Fisheries Science Center
5. Research Priority for this Proposal:	Research Priority #2
6. Project Duration:	2 years
7. Total Funding Request:	$151,437
8. Year 1 Request:	$97,176
9. Year 2 Request:	$54,261
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18. Institutional breakdown of budget:	100% SWFSC

Background

We are all aware that Earth's climate is expected to change substantially in the next 50 years, with an increase in global mean temperature of as much as 1.6°C (*1*). How organisms and ecosystems respond to climate change will affect the productivity of harvested populations, biodiversity, and conservation of threatened species (*2-3*). Predicting responses to climate change is therefore of critical importance. The proposed work addresses this need by developing a robust framework for predicting demographic responses to climate change.

Much current research on how climate change will influence organisms and ecosystems has focused on predicting shifts in primary productivity and species distributions (e.g., *3*). However, for many marine species, although range shifts on the order of 10- 100 KM are likely these changes primarily reflect changes in the margins of populations -- The majority of the species' range remains the same. Thus, although range shifts are certainly important, we cannot afford to neglect the pervasive changes that will occur within the center of species' ranges, such as shifts in relative abundance and other demographically relevant traits.

For most of the species we manage (specifically those that are not highly migratory), management actions are typically restricted to fixed locations dictated by political boundaries rather than ecological relevance; such 'management units' are unlikely to move as ranges shift. There is, therefore, a clear need to predict the local effects of climate change on spatial scales that are relevant to management.

Life history characters, such as maturation age, fecundity, and lifespan, are major determinants of population dynamics and sustainable harvest rates (e.g. *4*). However, predicting responses of these traits to climate change is typically feasible only for well-studied species or those with long-term data. Since such data are not available for many species, there is a clear need to develop novel tools that allow us to leverage information across taxa while rigorously accounting for uncertainty in predicting responses to climate change.

One possible framework for doing so comes from the metabolic theory of ecology (MTE, *5*). The MTE postulates that physiological rates scale as the ¾ power of body mass and follow Boltzmann -Arrhenius temperature dependence with activation energies of approximately 0.6-0.7 eV (e.g. *7*). There is considerable empirical support for the general predictions of the MTE and applications have ranged from explanations of developmental time, to macroecological patterns including global-scale analyses of trophic cascades, species diversity, population density, carbon turnover time (*6-9*). However, to be useful in predicting local, species-specific responses to climate change, we need to know how temperature affects traits **within species**. However, most applications of the MTE have been fairly coarse, **cross-species** comparisons, leaving open the question of whether the MTE typically applies within species.

Recently, we showed that across 74 ectotherm species, ranging from copepods and krill to fish, that within species the relationship between log-lifespan and the local mean temperature is consistent with predictions of the MTE (Figure 1, *10*). Although there is considerable variation among intercepts, the slopes of the regression lines are remarkably uniform. Moreover, the distribution of slopes from field data is nearly identical with the distribution of slopes based on

lab studies. Thus, despite spatial variation in food availability, the diversity of predators, and local adaptation, the ***average*** relationship between temperature and lifespan is fairly predictable.

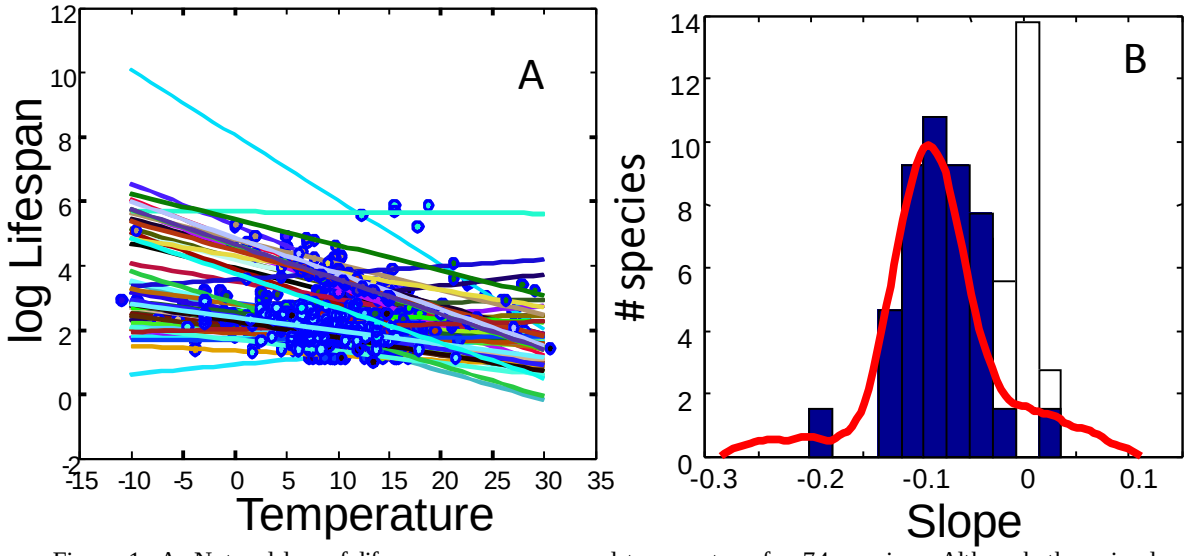

Figure 1. A. Natural log of lifespan v. mean annual temperature for 74 species. Although there is clearly variation around the regression lines, higher order polynomials did not fit significantly better. B. Histogram of regression slopes. The blue bars are counts for all non-zero regression slopes. The white bars are those that were not significantly different from zero. The red line indicates the histogram of slopes obtained from laboratory studies of lifespan and temperature. The clear concordance between slopes from the field (bars) and slopes from the lab (line) strongly suggests that other factors (predators, food) do not change the ***average*** response to temperature.

This result suggests that it would not be totally unreasonable to use the MTE to make spatially-explicit, worldwide predictions for changes in lifespan driven by anticipated warming over the next 50 years. For example, using the Community Climate System Model's (http://www.ccsm.ucar.edu) 10-year surface temperature averages from 1990 to 1999 as the baseline and the predicted 2045-2054 averages as the endpoint (A2 scenario), we can map the expected % change in lifespan. This relatively simple exercise reveals the surprising result that lifespan will decrease on average by 12.5% -17.5% worldwide with reductions of 10-20% throughout most of the world and changes of up to 40% at high latitudes (Figure 2).

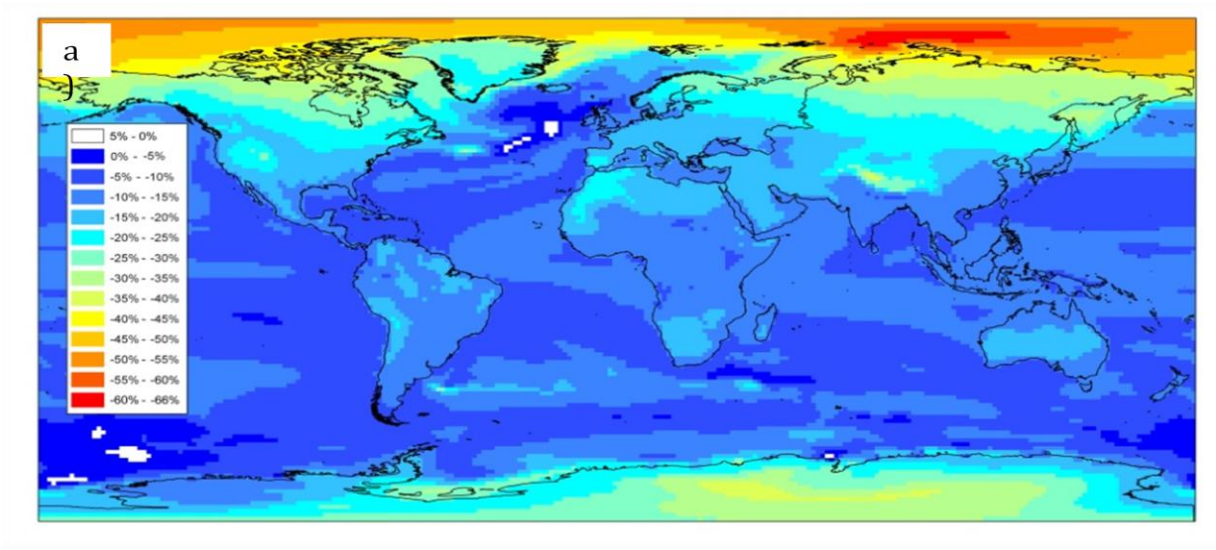

Figure 2. Percent change in ectotherm lifespan over the next 50 years based on IPCC A2 projected surface temperatures.

Since mean lifespan is the inverse of the average mortality rate, this suggests that substantial changes in management will be needed to compensate for climate-driven changes in life histories, particularly in middle- and high-latitude stocks. Moreover, increases in mortality tend to magnify recruitment fluctuations and the apparent nonlinearity of population dynamics (*11*). The MTE provides a first order approach to incorporating the likely changes in mortality into management and recovery plans. This proposal will extend these results for lifespan to other demographically relevant life history traits.

Approach

Using the MTE as a conceptual foundation, the goal of this proposal is to establish a framework for predicting the first-order response to climate change in other demographically relevant life history characters, specifically growth, fecundity, age and size at maturity, and natural mortality. Numerous prior studies have demonstrated that these vital rates are strongly correlated and driven, in part, by temperature (e.g. *12-13*). What is lacking is an overarching synthesis of geographic variation *within* species across a wide range of taxa that can be used to make robust generalizations of how under-studied species will respond.

The traits listed are all useful in constraining standard stock assessment models. In addition, estimates of population growth (r_{max}) and carrying capacity (K) are the frequently the cornerstones of data-poor assessment methods. Savage et al. (*19*) derive zeroth order predictions for the mass and temperature scaling of r_{max} and K. Using the scaling relationships we infer for life history traits, we can extend Savage's analysis to make robust first order predictions about climate-driven changes in r_{max} and K.

Step 1) Compile all available field estimates for species with data from multiple populations and use GIS to characterize the local thermal regime. One might expect that such a database already exists. However, databases that contain life history characters generally ignore trait variation within species and databases that focus on geographic variation generally ignore life history characters or are limited to a handful of species. We initially hoped that FishBase would be a good place to start, but the data are poorly georeferenced within species.

We will make use of several sources of data: We will begin by georeferencing and integrating existing databases. These include FishBase, Fish Traits, the life history databases maintained by the AFSC and Pacific Shark Research Center, CA DFG's nearshore fishes life history database, DATLife, and AnAge. We have already begun georeferencing the citations in FishBase. Second, we will scour the primary literature for publications reviewing geographic variation in life history traits. We have already made substantial progress in this direction, though more effort is clearly needed. Third, we will collect and assimilate gray literature reports from state agencies.

Through these efforts we expect to be able to obtain complete data (defined here as at least 5 locations with information on growth, fecundity, maturation age and size, and lifespan or mortality) on at least 100 species. In addition, we expect to obtain partial data (a subset of traits with limited spatial coverage) on hundreds more species.

Step 2) Characterize the thermal environment. For each location represented in the trait database, we will characterize the thermal environment. Although applications of the MTE typically use only the mean temperature, niche models frequently incorporate additional indices, such as the variance in temperature or the minimum and maximum temperatures (e.g. 14). These indices will be obtained from global climate databases maintained by NOAA, NASA, WorldClim, etc as appropriate.

Step 3) Synthesize all available trait and temperature data. To begin, we will evaluate the validity of the Boltzmann-Arrhenius temperature dependence of the MTE for each trait. For each species with sufficient data, we will test the Boltzmann-Arrhenius temperature dependence against higher order models and models that include temperature x mass interactions. We will also test the other thermal environment indices (min, max, variance, etc) collected in step 2.

After establishing whether the MTE is an adequate approximation within species we will construct a hierarchical model that accounts for phylogeny and spatial autocorrelation. The value of this framework is that it will allow us to make reasonable predictions for the species for which we only have partial data sets. We will extend the methods described by Ives and Zhou (*15*) to handle multivariate responses. The general framework is a Bayesian hierarchical model analogous to general least squares. That is (assuming that the basic MTE model is adequate)

$$\boldsymbol{y}_{i,l} = \boldsymbol{\mu} + \boldsymbol{\alpha}_{i,l} + \boldsymbol{\beta}_{i,l} \ln\left[M_{i,l}\right] + \frac{\boldsymbol{E}_{i,l}}{T_l} + \boldsymbol{\varepsilon}_{i,l}$$

Where $\boldsymbol{y}_{i,l}$ is the vector log-trait values for species i in location l, M is it's mean size (mass), and T is the mean annual temperature in location l. The vectors $\boldsymbol{\alpha}_{i,l}$, $\boldsymbol{\beta}_{i,l}$, and $\boldsymbol{E}_{i,l}$ represent the intercepts, mass-scaling exponents, and 'activation energies' for each trait. Under the standard MTE, only the intercepts are expected to vary among species and locations. However we adopt a more general framework here to test the idea of constant scaling and temperature dependence. The errors $\boldsymbol{\varepsilon}_{i,l} \sim N(0, V)$ are assumed to be independent across traits, species and locations. Phylogenetic and spatial autocorrelation are accounted for in the priors on $\boldsymbol{\alpha}_{i,l}$, $\boldsymbol{\beta}_{i,l}$, and $\boldsymbol{E}_{i,l}$. Specifically, $\boldsymbol{\alpha}_{i,l} \sim N(0, C_\alpha)$ in which $C_\alpha$is obtained as the tensor product of separate trait (T), spatial (S) and phylogenetic (P) covariance functions, $C_\alpha = T \otimes S \otimes P$. A similar specification with independent hyperparameters will be used for the mass and temperature scaling vectors. The trait covariance, T, will be assigned a vague inverse Wishart prior. We will use the standard specification for the phylogenetic covariance matrix based on a Brownian motion (*15*) with approximate branch lengths obtained from the Open Tree of Life project (www.opentreeoflife.org, *16*) or the Integrated Taxonomic Information System (www.itis.gov). S will be given by the Matern covariance function widely used in spatial statistics (*17*). This model can also be generalized by allowing taxonomic variation in the trait covariance matrix (18). We will also test simplified models in which spatial and / or phylogenetic variation for each parameter is removed.

After fitting to the available data, predictions for species with incomplete or missing data can be made through this framework using standard tricks for hierarchical, random effects, and Gaussian process models (see e.g. 15, 17). Doing so requires that we can input the mean size, temperature, location, and taxonomy for the species to be predicted. To handle cases where the mean size for the predictee is unknown, we will construct an auxiliary hierarchical random effects model for mean size that accounts for phylogenetic and spatial autocorrelation.

Step 4) The final step is to take the best fitting hierarchical Bayesian MTE model and GCM model output to make species-specific maps of life-history changes over the next 50 years. We will evaluate results for several of the IPCC scenarios to account for uncertainty in GCM predictions.

Benefits

This proposal specifically addresses FATE research priority #2 in that it will develop spatial models of climate effects on growth, maturity, mortality, and fecundity. By constructing statistical models that explicitly account for phylogeny as well as space, we will leverage information across related species allowing improved predictions for stocks for which we have sparse information. This will be particularly useful for managing data-poor fisheries.

Coupling these statistical models with global climate forecasts will allow us to construct spatially explicit predictions of demographically relevant traits over the next 50 years. This will be particularly useful for evaluating whether strategic changes in management are needed to account for climate change.

In addition, this database will allow us to address some basic science questions as well, including: how well to classic life history invariants hold up when looked at within species? Does the MTE generally work within species in the field? Is there a phylogenetic signal in the mean response to temperature? Are MTE predictions within species biased for heavily exploited populations? Are the deviations from the MTE driven by fishing mortality predictable?

Deliverables

- A global database of spatially-explicit life history characters and local environmental drivers
- Spatially explicit estimates of life history traits, r_{max} and K for all 'data poor' species
- Global projections of climate-driven changes in life history traits.
- At least 2 peer-reviewed publications and conference presentations
- Final report to FATE

Year 1	Year 2
○ Identify and incorporate gray literature estimates of life-history characters ○ Targeted acquisition of complete trait sets for 100 species ○ Complete creation of database ○ Present at annual FATE meeting.	○ Develop models to integrate across taxa ○ Test predictions of MTE for each trait ○ Produce 50 year projections using several climate scenarios ○ Publish papers ○ Present at annual FATE meeting

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