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Introduction

Management of native trout in the Flathead Basin Lake-River system has become a difficult issue due to a major shift in the the systems dynamics. This shift occurred with the dramatic increase in abundance of a non-native species, *Mysis Relicta*. Montana Fish, Wildlife & Parks and the Confederated Salish and Kootenai Tribes have the stated goal to continue managing for native trouts in the lake while maintaining the popular lake trout fishery, however they believe that the lake trout levels control bull trout abundance which may make management for both species problematic [12]. The current management strategy is to slowly ramp up lake trout harvest until a response in native species population levels is detected. We propose using a community model focused on the lake trout, bull trout, mysis interaction as a way to not only understand the change in dynamics but as a tool to investigate possible management decisions and to possibly predict their implications. This analysis is to be supplemented by intensive sampling of the lake in order to provide model validation. This will increase parameter estimation precision and allow adaptive changes to the dynamics model to be incorporated over the sampling time.

The Flathead Basin system has been the focus of some study over the past decade due to managers efforts to preserve the native trout populations, and because of researchers interest in understanding the system dynamics change [14]. The introduction of mysis into the system has presumably caused a shift in the communities species composition. This freshwater shrimp has made available much more biomass directly to the top trophic levels in the system. A corresponding shift has been a large increase in lake trout abundance and a coupled decrease in abundance of the native trouts in the system: bull trout and westslope cutthroat trout. A community model would be a synthesis of the known components of the system and may provide insight that analysis on the individual pieces may not be able to achieve.

By integrating the estimates for known quantities and interactions with those that are unknown we can potentially answer some qualitative questions regarding what effects management decisions might have on the species of interest. This approach will not only allow us to explore current ideas on the nature of the bull trout-lake trout-mysis interaction, but will allow us to investigate what types of data might be useful to collect for future work. Due to the unknown nature of these relationships we will treat other species influences on the species of interest as a black box, where possible interactions can be investigated. Identifying where the gaps in our knowledge are would lead to decisions which would improve management efforts in the fishery. Knowledge of what the most important variables are, what resolution of data is necessary to detect changes in populations and what kinds of aggregation of the data maybe useful for optimizing management efforts in the system but may be analyzed using this type of approach.

This analysis would provide insight on scenarios which are of interest to the management agencies on the Flathead Lake and River system. It would be the goal of the analysis to provide usable and interpretable results to those agencies as well as to provide a framework for future management decisions in the system. This would be developed as an open tool for use by the involved agencies We believe this is an appropriate analysis to do both because of the number of unknowns in the system make it difficult to understand consequences of management decisions and because the roles of species on other trophic levels are integral to the survival of the native trouts. The dynamics model and associated validation process aim to provide managers with a flexible tool that can be used to

Literature Review

The Flathead system has been studied for the last two decades fairly intensely. The Flathead Biological Station has run a number of studies, mostly focused on the lower levels of the Flathead food web. Population estimates of the mysis [14] have shown that mysis peaked in the mid 80's and have since stabilized. Corresponding decreases in bulltrout redd counts were evaluated by Ponciano et al [submitted] at the time of the large increase in the mysis population. Mysids feed on cladocerans such as *Daphnia Thorata* which are also fed upon by native salmonids. Experimental work by Spencer & Ellis suggest that bottom up controls regulate zooplankton populations. This bottom up control may be what is controlling mysis abundance as well, however work by Wicklum [12] suggested that mysis may be able to undergo to a five-fold increase in abundance.

Chess & Stanford [2] suggest that juvenile Westslope Cutthroat may be especially vulnerable to competition with mysids. The mysids have been observed to undergo prey switching from cladocerans such as the daphnia to copepods making them resilient to changes in the food web, and so may keep high pressure upon daphnia even when prey populations are low. Because bull trout are of larger size when they enter the lake their prey base consists mostly of other fish [1] and this interaction may have little impact upon their abundance. Energetics work by Beauchamp [1] showed that a significant portion (1216 $\frac{MT}{y}$) (~25%) of the diet biomass of all length classes of lake trout is comprised of mysids (sample size = 496), while lake whitefish consumed 985 $\frac{MT}{y}$ (sample size not reported). Combined they consumed an estimated 55% of the annual mysid production in the lake, however these estimates also predict that a 3-5 fold increase in mysis should occur, consistent with Wicklum's conclusions. The absence of this increase may imply that the estimates are significantly off or that there are important processes in the lake which have not been identified. Lake trout also had significant consumption on whitefish so decreasing lake trout populations may have uncertain consequences on both whitefish and mysids. Confidence intervals on estimates were not reported and they are likely to be highly uncertain. Other energetics work by Bennet & Steinhorst (referenced by [12]) claims that a population of 1200-1300 northern pike may consume 2900 juvenile bull trout and 6900 westslope cutthroat trout annually. Pike consumption may then be an important factor in bull trout population dynamics. Work by Staples et al [15] used redd count data and gill net catches to describe life history factors that influence bull trout abundance. Their analysis suggested that decreases in sub-adult survival correspond to proportional decreases in the populations growth rate. Bull trout populations have been estimated to be above defined secure levels and stable by Muhlfeld et al [9] using redd counts which have been conducted every year since 1979. Secure levels were defined by a risk assessment analysis done by the associated management agencies [3]. Juvenile abundance in natal streams has been studied over this time period as well, however it is unclear at what level the lake trout are being depressed by current measures and how those measures have contributed to the persistence of the bull trout population.

Interesting and possibly relevant interactions in the lake may contribute to the persistence or suppression of the bull trout population, although is unclear which of those interactions may have potential management consequences. It is unknown what the effect of reducing the mysis population may trigger in the community composition. Yellow Perch and Lake Whitefish may contribute to depressing mysis levels, however, the levels at which they must be present to do so is unclear. Although the complete nature of the mysis interaction with other organisms in the lake is unknown, it probably is an important factor in the current species abundance levels in the lake.

Lake trout have also been discovered in Yellowstone Lake, another nonnative environment for these fish. Here the lake trout have been actively managed through gill netting. This gill net data was then used to estimate population structure of the lake trout and to estimate the impact that these fish might have on the native cutthroat trout. A total of 15000 lake trout had been removed as of 1999, and the impact that these fish may have had on native cutthroats could be substantive. Lake trout population structure has indicated a shift over this period of gill netting possibly due a change in lake trout abundance [11]. Studies have looked at the possibilities of a trophic cascade occurring in the Lake Yellowstone food web, possibly impacting grizzly bears and other consumer species which use the cutthroat trout as an energy source [7, 10]. These are similar to shifts that have been seen in the Flathead system [14] and may provide an illustrative example of how to manage the lake trout issue in the Flathead.

Data & Methods

Many components of the system have little or no data due to the scales and number of species involved. Bull trout redds have been studies from 1979-current and have been used to infer the current secure and stable levels. Variation between years has stabilized indicating stable populations for the time being. Gill netting data is taken in the spring and done in 5 fixed locations on the lake using a total of 15 nets (3 per location). This data has been collected 1981, 1983 and 1996-present. Catches post mysis introduction have indicated that abundance of bulltrout relative to lake trout has undergone an a reversal, from a lake dominated by bull trout to one dominated by lake trout. However this data is not sufficient to build an accurate picture of community dynamics. Instead our proposal is meant to identify issues important for further understanding of the system and to explore how the components of the system fit together to make a whole.

Gill net data on the system is classified into length classes, so a length class

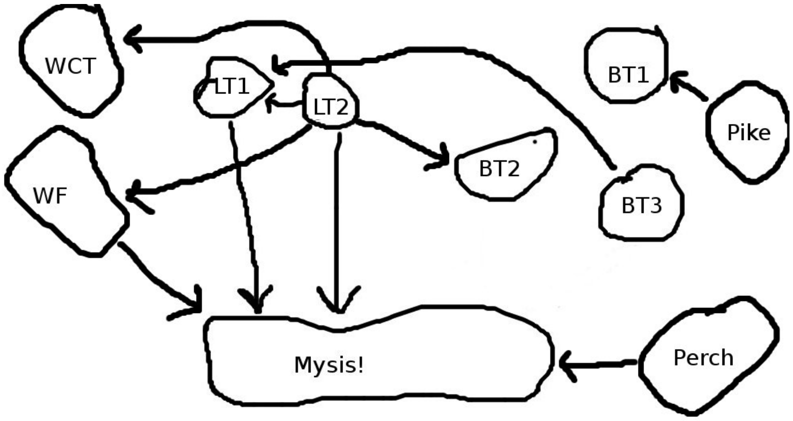

Figure 1: Artistic Interpretation of food web, documenting possibly relevant interactions in the Flathead Lake Community towards bull trout population trends. WCT=Westslope Cutthroat, BT=Bull Trout, LT=Lake Trout, WF=White Fish. Higher numbers correspond to higher size classes. include lower trophic levels

model is appropriate both from the data and from a biological perspective. Population abundance of natives and lake trout has been estimated [3], however the estimates are not precise and confidence intervals vary widely. The challenge, then, is to integrate these order of magnitude estimates into the known dynamics of the system and make predictions for what relative changes in composition might mean for native trouts. Estimates for predation by Lake Trout on native trout can start with Beauchamps energetics work, however because the salmonids provide rare opportunities for predation due to their low densities, these estimates are certain to be problematic.

Each species has a population given at time $t+1$ by $N_{ij}(t+1) = N_{ij}(t)f_{ij}(\cdot)$ where $f_{ij}(\cdot)$ is some growth model appropriate for the i^{th} organism and the j^{th} length class. A simple case is the exponential model where $N(t+1) = r_0 N(t)$. Here r_0 is an intrinsic population growth rate and given by the difference of the birth and death rate. This model can incorporate predator prey interactions in a simple way by letting kills happen proportional to the number of predators and prey. H is the number of prey and P is the number of predators then $H(t+1) = H(t)g(H(t)) - aH(t)P(t)$, $g(H(t))$ is an appropriate density dependence relation and $aH(t)$ is a functional response which can be modified according to the biology. The predators can then be modeled as $P(t+1) = e(aH(t)P(t)) - sP(t)$, where the birth rate is scaled by e, the efficiency of turning prey into new predators and s gives a death rate for the predators. Multiple species interactions can be incorporated in the same way. One way this two species model can be written as a matrix is the following way:

$$\begin{pmatrix} H(t+1) \\ P(t+1) \end{pmatrix} = \begin{bmatrix} g(H(t)) & -aH(t) \\ eaP(t) & -s \end{bmatrix} \begin{pmatrix} H(t) \\ P(t) \end{pmatrix}$$

where off diagonal terms are interactions between species. In this form it is easy to see how this model can be generalized to multiple predators, multiple prey species and different length class structures.

The crux of the management plan in the Flathead System is that removal of lake trout is beneficial to the native salmonids, however this causal chain has not yet been demonstrated and removal of the lake trout may increase competition between subadult salmonids and mysis for zooplankton on which the subadults rely on before switching to macroinvertebrates or other prey fishes. If lake trout are suppressing mysis populations, reduction of their populations may be detrimental to the already low salmonid populations. Our model can investigate this possibility by decreasing lake trout densities and observing mysis and native trout responses.

Heterogeneous densities of fish over time may provide predators with opportunistic feeding behavior. Bull trout migrate primarily in the spring during high flows. Observations of predation upon juvenile bull trout migrating from natal streams to the lake by lake trout is evidence that the lake trout may be opportunistically exploiting the smaller size class bull trout during periods when they are at high concentrations. There is also evidence of a relatively small number of pike taking around 3000 juvenile bull trout and 7000 westslope cutthroats [Bennet & Steinhorst referenced by [12]]. The consequences of this sort of behavior can be investigated by modeling intense predation over short time periods on the subadult bull trout length class.

Spatial heterogeneity in diet, growth and distribution [8, 5] have been observed in lake trout populations, however these considerations have not been considered in previous estimates and it is unknown how this spatial structure would affect estimates of lake trout abundance or if there may be potential consequences for native species. Spatial structure in lake salmonids populations has been demonstrated with respect to depth. Depth is commonly associated with the temperature gradient of the lake, but in a lake as large as Flathead we might expect spatial structure in fish populations. The work in Lake Ontario

[5] has demonstrated such structure in the lake trout populations but it is unknown how these structures might play in to population interactions between lake trout and other fishes.

Model Validation

The connection between models and data can go both ways. The model validation process is the testing of a model once it has been built. As well as using data to estimate model parameters we can use the model to make predictions about future system states and these predictions from the model can then be compared to real data. Further refinements of the model can then be performed or invalid assumptions in the model may be identified and reconsidered. Because such validation will depend on the conclusions from the modeling analysis a general outline for this validation can be proposed but specifics will be dependent on outcomes from the dynamics analysis. Observations from a combination of gill netting and sonar data can be combined to form estimates of species composition and size structure within populations. These estimates can then be used to validate predictions from the community model. Species and length proportions estimated from the gill netting data and be applied to sonar data to get a sample of high sample size and with estimated species/length compositions. A time series analysis of the data is appropriate and parameters can be estimated using the Kalman filter and maximum likelihood estimation [13, 4, 16]. The Kalman filter allows the model to incorporate both observation error and stochasticity. Decomposing the error into two sources will allow us to identify areas for improvement in the sampling design. To illustrate the procedures consider the following example, if the community model identified the lake trout - whitefish interaction as an important driver for the community structure we might try to accurately estimate the populations and the parameters of these species in the model. We can start with the population model for the two species by extracting the relevant entries and interactions from the community model. The population at time t can then be written as $N_{ij}^{t} = N_{ij}^{t-1} f_{ij}(\cdot) + w_{ij,t}$, where $f(\cdot)$ will contain growth rates and all necessary interactions with other age classes and species of interest, and $\mathbf{w}_t$ is multivariate Gaussian error, $\mathbf{w_t} \sim MVN(\mathbf{0}, \mathbf{\Sigma}^{\mathbf{w_t}})$. The relationship between observed fish from the combined gill netting and sonar data is then assumed to be proportional to the true population, written as $\mathbf{O_t} = \mathbf{u_t}\mathbf{N_t} + \mathbf{v_t}$, where $\mathbf{v_t} \sim MVN(\mathbf{0}, \mathbf{\Sigma}^{\mathbf{v_t}})$.

These equations can then be incorporated into the Kalman filter framework and the maximum likelihood estimates can then be obtained. Once estimations have been made predictions for the next year can be made and in this way we can monitor the efficacy of the model as the sampling is carried out.

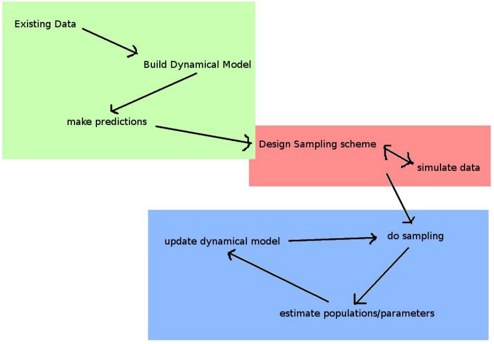

Figure 2: flowchart describing the modeling and sampling steps

Design of the sampling scheme is ultimately dependent upon the inference that is of interest. Sampling effort and design can be tested in simulation studies. Sampling error has been investigated in the Great Lakes using similar techniques as proposed [6] and can be used in the generated observations to observe the effects of different sampling efforts on the inference. This analysis may not lead to an optimal sampling design but the design can be improved in this way. If the inference cannot be made to a prespecified degree of precision given personnel, temporal and financial constraints, alternatives will have to be explored.

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