**Disentangling the Impact of Climate Warming and Fishing on the Biomass of Freshwater Fish Populations**

**Introduction:**

Climate change, manifested primarily by the increased global mean temperature, can significantly alter the freshwater habitats of inland lakes. Such warming can then affect the stock biomass of fish populations that inhabit these waters through a series of physiological, biochemical, and ecological processes (). Warming can directly impact the seasonal thermal structure of inland lakes (), exposing certain fish populations to temperatures outside their species-specific optimal ranges, while making thermal conditions more suitable for other populations. Other common warming-related natural processes that also affect stock biomass of freshwater fish populations include decreases in dissolved oxygen (), reduction and shortening of ice cover (), plankton bloom phenology (), and toxic algae blooms ().

Responses to warming are likely to vary inter- and intraspecifically. Warm- and cold-water species may respond to warming in opposite directions based on species-specific thermal requirements (). Populations of the same species may respond differently to warming, depending on individual properties such as geographic position or local adaptations to thermal regimes (). Illustrating among- and within-species variation in responses to warming, a meta-analysis of global marine fish and invertebrates revealed that populations benefiting from historical ocean warming were roughly offset in number and magnitude by those that were negatively affected (). Although the general effects of warming on freshwater fish species from different thermal guilds have been documented (), the potentially heterogeneous effects of warming on the stock biomass of individual populations are less clear on regional or global scales.

One challenge in evaluating the warming effect on freshwater fish stock biomass is the fact that warming-related environmental changes interact with local anthropogenic activities to create complex and entangled effects on fish population dynamics (). For the target species of recreational or subsistence fisheries, angler harvest constitutes the most widespread source of stressor for freshwater fish populations by directly removing certain numbers of fish from the populations persistently. As a result, failure to accurately disentangle the effects of changes in fishing pressure and temperature on fish stock biomass can often lead to misattribution for the cause of stock size fluctuations ().

Separating the impact of fishing and climate warming on freshwater fish stock biomass is not only of interest to scientists but also critical to fishery managers to identify optimal management strategies to grapple with the effects of both stressors (). Local and regional management agencies in the US have developed adaptation strategies (e.g., regulating harvest or stocking) to keep the fisheries sustainable and to partially mitigate the effects of warming (). Although it is widely accepted that slowing the pace of climate warming by collectively reducing greenhouse gas emissions is the ultimate solution to conserve most fish and fisheries globally (), accurately quantifying the respective contributions of fishing and warming to changes in fish stock biomass can help managers decide on appropriate and practical measures to regulate variables that can be locally managed.

Despite the often limited human resource compared with the large number of waterbodies to be monitored, the relevant agencies or commissions in each state closely monitor many inland fish stocks that are socioeconomically or culturally vital to local communities by exploiting appropriate data collection methods (e.g., survey lakes on a rotational basis). We collated a data set for 309 fish populations from five Midwestern states in the United States that can be used in a novel temperature-dependent population dynamic model. The model was developed with an intention of addressing the challenges of fitting traditional fishery stock assessment models to typical inland fisheries data (e.g., inconsecutive and imprecise annual harvests). Simulation tests and sensitivity analysis were conducted to evaluate the robustness of the model to estimate the effect of temperature on fish stock biomass. Finally, we disentangled and compared the effects of temperature variation and fishing on fish biomass by simulating two scenarios that assume the absence of fishing or warming, respectively.

The study aims to contribute to understanding the respective impacts of fishing and warming on stock biomass of freshwater fish populations at a relatively large regional scale. The Midwest of the United States was chosen as there are diverse freshwater fish species, many of which support prized recreational and subsistence fisheries (), and which have endured rapid warming over the past decades (). The approach reported here has the potential to be applied to inland fisheries in other regions where similar data are available, and to enhance the understanding of this long-standing scientific question on a global scale.

**Materials and Methods:**

*1. Data sources and data characteristics*

*1.1 Relative biomass index*

Time series of relative biomass indices were derived for each population from the fishery-independent biological surveys conducted by the Department of Natural Resources of each state. Survey protocols vary between management agencies, and survey methods often differ depending on the purpose of the survey. Therefore, we consulted relevant experts from each state who were familiar with their respective survey programs and obtained the relative biomass indices that best reflected the temporal changes in stock biomass for each population (Tab.S1 in the supplementary material).

*1.2 Recreational harvest*

Total recreational harvests were estimated based on the creel survey conducted by Department of Natural Resources of each state. Data were collated and stored in the CreelCat database (<https://creelcat.shinyapps.io/CreelCat/>). The data were downloaded from CreelCat on 4 June 2022. Unlike large-scale commercial fisheries, where accurate daily catch records are required, estimated recreational harvest data based on voluntary angler interviews are considered less precise. Therefore, we treated the recreational harvests as observations that are subject to observation error instead of known quantities in the model.

*1.3 Tribal harvest*

The Great Lakes Indian Fish and Wildlife Commission (GLIFWC) collected tribal harvest data. All tribal fishing operations were under observation, and all fish harvested were recorded. Therefore, tribal harvests were treated as known and accurate quantities.

*1.4 Stocking biomass*

The time series of the biomass of stocking fish for each population were extracted from stocking report released by the Department of Natural Resources of each state. Stocking biomass was treated as known and accurate quantities.

*1.5 Environmental data*

The environmental data for each lake came from a process-based lake water temperature model (). The data were verified and released by the U.S. Geological Survey. Growing degree days, the sum of the thermal energy above the base temperature (5℃ here) for the lake surface (GDDs\_5), was used as the climate warming index in this study. GDDs\_5 was selected for this study as it reflected the cumulative thermal energy throughout the year and was commonly used for describing the thermal scope for fish growth (). To verify our selection of warming index, we also checked the correlations of GDDs\_5 with other warming indices including growing degree days with base temperature at 0℃ or 10℃, open water duration, peak temperature of the year, and lake surface mean temperature of each month (SI.1 in the supplementary material).

*2. Model development*

*2.1 The Pella-Thomlinson surplus production model*

The stock biomass of a fish population after a certain time interval (e.g., a year) is equal to the stock biomass before that time interval plus the recruitment and somatic growth of individual fish minus mortality due to natural processes and fishing (if present). Growth in stock biomass follows a density-dependent logistic pattern. The Pella-Tomlinson model commonly used to describe the fishery population dynamics can be written as follows ():

(1)

(2)

where *k* is the carrying capacity; *r* is the intrinsic growth rate of the population; is stock biomass at year *y*; *Cy* is the catch in year *y*; *Iy* is the relative biomass index in year *y*; *q* is the catchability coefficient; *ȵy* are observation errors, assumed to follow a normal distribution, i.e., , is the variances of observation errors; in equation (1) represents the surplus production in year *y*; *m* is a shape parameter that determines at what *B/K* ratio maximum surplus production would be attained. When the shape parameter *m* is fixed at two, the model is equivalent to the Schaefer surplus production model, with the maximum surplus production attained at half of the carrying capacity. The Pella-Tomlinson model is equivalent to the Fox model if shape parameter *m* approaches one, resulting in maximum surplus production attained when biomass equals 0.37*k*.

*2.2 The net effect of warming on stock biomass of fish populations*

Surplus production is a net gain in stock biomass in the absence of fishing, where the increase in biomass comes from recruitment and somatic growth of individual fish and the decrease in biomass is due to natural mortality. Warming may impact recruitment, individual fish growth, and natural mortality of the same population in different directions and magnitudes. Here, rather than separately evaluating the effects of warming on the three dimensions mentioned, we attempted to quantify the net effect of warming on overall surplus production.

*2.3 A modified temperature-dependent surplus production model*

We modified the Pella-Thomlinson surplus production model to account for stocking of recreational fish stocks, to address the issue of nonconsecutive and imprecise recreational harvest data, and to account for the impacts of temperature on productivity. Annual recreational harvests were not treated as known and accurate quantities in the dynamic model, but as observations subject to observation error. We then incorporated a multiplicative temperature effect term into the dynamic model to quantify the effect of warming on surplus production. The modified temperature-dependent surplus production model is written as follows:

(3)

(4)

(5)

where is the parameter of warming effect; represents the growing degree days in year *y*, is standardized and centered on the mean (so that positive suggests positive impact of warming on surplus production and vice versa); is the instantaneous recreational fishing mortality in year *y*; and are the stocking biomass and tribal harvest in year *y*, respectively; is the observation error associated with recreational harvest, is assumed to follow the normal distribution, i.e., and is the variances of observation errors; Other parameters are the same as in the traditional Pella-Thomlinson model.

Finally, we reparametrized the population dynamics model by using the ratio of biomass over *k* (*P*) as the changing states instead of biomass (*B*) to improve the performance of model fitting (). The reparametrized model is written as follows:

(6)

(7)

(8)

*3. Model fitting*

*3.1 Prior distributions specification*

The model parameters were estimated using the Bayesian method. We used non-informative or weak-informative prior distributions for all the parameters. The prior range of intrinsic growth rate *r* were determined based on the species-specific resilience, which indicated the capacity of a population to recover to its original state after disturbance. (Tab.S2 in supplementary materials). For the carrying capacity *k*, the lower bound of the range was set equal to the maximum harvest, and the upper bound was 10,000 times the maximum harvest (a wider range was tested in the sensitivity analysis). Since the log-normal prior was considered to have better convergence properties than the uniform prior, the ranges were converted into log-normal priors with the mean and standard deviation calculated by the following functions:

(9)

(10)

where and are the lower and upper bound of the range.

The catchability coefficient *q* was given an improper prior (i.e., p(q)∝1/q). *p\_initial* (B/k for the initial year) followed a Beta distribution due to its desirable property of being bounded by [0,1] for ratios. Warming effect *θ* followed a normal distribution with mean equal to 0 and standard deviation equal to 1 (prior distribution for *θ* with a larger standard deviation was tested in the sensitivity analysis). The logarithm of the shape parameter *m* followed a skew normal distribution with the intention of penalizing small values of *m* that imply implausibly high population growth rates at very low population sizes. Instantaneous fishing mortality *F* was assigned an exponential distribution that corresponds to a uniform prior bounded by [0,1] on the proportion of biomass removed by fishing. The variances of observation errors associated with relative biomass index and recreational harvest followed an inverse gamma distribution that was conjugated to normal distribution.

*3.2 Model execution and convergence*

We assumed there was no process error, hence we used the observation-error estimator instead of a state-space model (the consequence of violating of this assumption was checked in the simulation study). Model fitting was performed using Stan through the R package “rstan” (). Four chains of 20,000 iterations each were run, with the first 10,000 designated as warmup. This process produced in total 40,000 posterior samples for each fitted model. The convergence of each model was checked by split- (<1.05) and trace plot of all parameters (). The number of effective sample (>0.01×iteration times), bulk effective sample size (>100/chain), tail effective sample size (>100/chain) were also checked.

*4. Model testing*

We conducted a simulation study to verify whether the temperature-dependent surplus production model was able to accurately estimate the parameter of warming effect. We simulated scenarios consisting of six different fishing patterns or biomass trends and the data collection process that generated nonconsecutive and imprecise CPUE and harvest. We also incorporated process error in the simulated operating model for the fish population dynamics and used observation-error estimator to fit the simulated data (SI.2 in the supplementary material).

*5. Sensitivity analysis and null model tests*

To check whether the model structure affected the estimation of warming effect, we tested the sensitivity of our results to the use of different surplus production models (SI.3 in the supplementary material). We also conducted a sensitivity analysis to check whether the estimation of warming effect was affected by prior specification (SI.4 in the supplementary material). To test whether the estimates of warming effect came out by chance as an artefact, we compared the results from base models with those from null models in which the time series of GDDs were randomly re-ordered (SI.5 in the supplementary material).

*6. Disentangling the effect of warming and fishing in changing stock biomass*

We compared the effects of temperature variation and fishing on fish biomass by simulating two scenarios that assumed the absence of fishing or warming, respectively. In the no-fishing simulation scenario, we set fishing mortality *F* to 0 and other parameters to their estimates. In the no-warming simulation scenario, we set warming effect to 0 (which is equivalent to setting GDDs\_5 of all years to the mean value) and other parameters to their estimates. We re-ran the population dynamic model and calculated the *B/k* ratio of the terminal year for both scenarios.