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8-12-2022

### Warming Overcomes Dispersal-Limitation to Promote Non-native Expansion in Lake Baikal

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#### Citation Information

Bowman, Larry L. Jr.; Wiczynski, Daniel J.; Yampolsky, Lev Y.; and Post, David M., "Warming Overcomes Dispersal-Limitation to Promote Non-native Expansion in Lake Baikal" (2022). *ETSU Faculty Works*. 967. <https://dc.etsu.edu/etsu-works-2/967>

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## Abstract

Non-native species and climate change pose serious threats to global biodiversity. However, the roles of climate, dispersal, and competition are difficult to disentangle in heterogeneous landscapes. We combine empirical data and theory to examine how these forces influence the spread of non-native species in Lake Baikal. We analyze the potential for *Daphnia longispina* to establish in Lake Baikal, potentially threatening an endemic, cryophilic copepod *Epischurella baikalensis*. We collected field samples to establish current community composition and compared them to model predictions informed by flow rates, present-day temperatures, and temperature projections. Our data and model agree that expansion is currently limited by dispersal. However, projected increases in temperature reverse this effect, allowing *D. longispina* to establish in Lake Baikal's main basin. A strong negative impact emerges from the interaction between climate change and dispersal, outweighing their independent effects. Climate, dispersal, and competition have complex, interactive effects on expansion with important implications for global biodiversity.

Keywords: Lotka-Volterra competition, zooplankton, temperature, endemism, meta-community model, dispersal

## Introduction

Changes in the ecology of a species in response to global change can lead to different community dynamics and species interactions (Chevin et al., 2010). Understanding how species respond to local temperature variation is only the first step; how this variation alters species' fitness via physiology, competition, and dispersal becomes crucial to making accurate predictions about future distributions (Vasseur and McCann, 2005; Amarasekare and Savage 2011; Amarasekare and Coutinho, 2014; Gilbert et al., 2014; Dell et al., 2014; Vasseur et al., 2014; Amarasekare, 2015). Species interactions become especially important when considering the likelihood of exotic or non-native species introduction and invasion into highly endemic systems (Thomson, 2005; Riley et al., 2008). One such system mediating changes in climate and invasions is Lake Baikal, a biodiversity hotspot and UNESCO World Heritage Site (Moore et al., 2009) located in Eastern Siberia, Russia. Lake Baikal hosts over 2000 species, nearly two-thirds of which are endemic to the region (Afanasyeva, 1998). Despite its status as a biodiversity hotspot, the critical link between the diverse phytoplankton assemblage of endemic diatoms and upper trophic levels, which includes the world's only freshwater seal, is a single dominant zooplankter, *Epischurella baikalensis*. *Epischurella baikalensis* an endemic, stenothermic zooplankter (previously *Epischura baikalensis*, Bowman et al., 2019) dominates the native zooplankton assemblage, comprising >90% of the pelagic zooplankton in Lake Baikal (Afanasyeva. 1998; Izmet'eva et al., 2016). This trophic position filled by *E. baikalensis* is therefore critically important to the regulation of phytoplankton biomass and energy flow to upper trophic levels.

Lake Baikal is warming at an alarming rate compared to its historical temperatures (Moore et al., 2009). With increased warming, there is a high likelihood that cosmopolitan

invaders will dominate the zooplankton assemblage in the lake (Hampton et al., 2008). *Epischurella baikalensis* is adapted to the cold waters experienced year around in Lake Baikal (Timoshkin et al., 2016), but also exhibits phenotypic plasticity and purported local adaptation to temperature across Lake Baikal (Bowman et al., 2018). The extremely species-depauperate pelagic zooplankton assemblage in Lake Baikal may provide an opportunity for cosmopolitan non-natives to outcompete endemic species (Dukes. 2002; Stachowicz and Byrnes, 2006) as the lake warms due to climate change (Hampton et al., 2008). *Daphnia longispina* (Beeton, 2002; Hampton et al., 2008; Timoshkin et al., 2016) has expanded into several of Baikal's shallower and warmer regions in the last 50 years, particularly in shallower regions such as Chivyrkuy Bay and the Selenga River delta (Hampton et al., 2008). *Daphnia longispina* has rarely been documented in the main basin of Baikal, perhaps because of the colder water temperatures found in the main basin (Sheveleva et al. 1995; Hampton et al., 2008). However, *D. longispina* has expanded more recently into surface waters in all basins of the lake and in neighboring Barguzin Bay and the more western Maloe More strait, although its reproductive success there remains unclear due to the sediment depth in the main basin being >1000m (Korzun and Pitulko, 2010). Climate change is expected to cause 2.7-6.4°C increases in the mean annual temperature of the epilimnion of the main basin of Baikal in the next 60-80 years (Moore et al., 2009). Despite the plasticity and adaptability exhibited by *E. baikalensis*, the predicted changes in water temperature may allow *D. longispina* to transition from the bays into the main basin where it could compete with *E. baikalensis*.

How *Daphnia longispina* and *Epischurella baikalensis* interact, especially in a warming climate, remains unclear. We assume that the two zooplankters will compete for habitat and resources or will differentiate along different niches within the lake, e.g., stenothermic *E.*

*baikalensis* will become restricted to deeper waters. *E. baikalensis* is currently found in all parts of the lake, including warm, shallow bays and from surface to max depth (Afanasyeva, 1998). Impacts, including nonlethal ones, of a *D. longispina* expansion into the main basin could dramatically change the Baikal ecosystem. For example, *E. baikalensis* provides a lipid-rich food source for the upper trophic levels of the lake, including many endemic fish, while *Daphnia longispina* would offer a different nutritional regime (Bowman et al., 2017). Thus, the greatest impacts of a *D. longispina* expansion may not be increased direct competition to other zooplankters but indirect effects for the fragile ecosystem broadly.

Here, we examine the role of climate, competition, and dispersal in determining the expansion success of a non-native in the Baikal zooplankton community using a spatially-explicit metacommunity model for the interactions between *E. baikalensis* and *D. longispina* along a transect from Chivyrkuy Bay into the main basin of Lake Baikal. We explore how these dynamics will shift with the predicted warming expected in Lake Baikal in the next 60-80 years (Moore et al., 2009). Our model is parameterized using empirical data from Baikal and the literature, representing one of few studies to harness horizontal spatial heterogeneity in lakes to predict expansion success under warming.

We found strong differentiation in the thermal niches of *E. baikalensis* and *D. longispina*, but we also found that dispersal and temperature play a key role in limiting the current extent of *D. longispina* into the main basin of Baikal. The predicted temperature increase in Baikal is sufficient to allow *D. longispina* to establish in the main basin, suggesting that even long-term, stable, and spatially-limited introductions may expand with global temperature increases.

## Model and Methods

Our approach incorporated theoretical and empirical data specific to Lake Baikal to build the model and then compared the model predictions to empirical data collected from Chivyrkuy Bay in summer 2013. Chivyrkuy Bay was selected as a location due to its temperature and depth gradient and where *Daphnia longispina* is found in highest abundance (Korzun and Pitulko, 2010; Figure 1). We then used a stepwise maximum likelihood approach to determine which model predictions match the assemblages we observed in Chivyrkuy Bay. Using the best model, we incorporated water temperature projections specific to Lake Baikal for the next 60-80 years (Moore et al., 2009) to predict future zooplankton assemblages and the likelihood of *D. longispina* invading the main basin of Lake Baikal.

## Model

We developed a metacommunity model to capture the salient spatial structure along the thermal gradient from Chivyrkuy Bay into the main basin of Lake Baikal. To match our empirical sampling schematic, we modeled six patches (Figure 2a) where the most bayward patch has a discrete invasion of *D. longispina* and where the most lakeward patch represents the main basin without further lakeward emigration or immigration. The most lakeward patch is representative of Baikal's open water zooplankton assemblage composed of >90% *E. baikalensis* by biomass (Kozhov, 1963). Because of the relative simplicity of the zooplankton community, we assumed both that intraspecific competition was the predominant limit to *E. baikalensis* prior to the introduction of *D. longispina*, and that *D. longispina* would be in direct competition with *E. baikalensis* where they overlap spatially. Unlike other members of the genus (and sister genus *Heterocope*, Bowman et al., 2019) which are carnivorous secondary predators, *E. baikalensis* is predominantly an herbivore and occasionally omnivorous (Moore et al., 2019). Because *E.*

*baikalensis* is the dominant zooplankter in Baikal, we assume that it will be in direct competition with *D. longispina* for all resources.

Each species exhibits a unique growth response to variation in environmental temperatures. We assumed both species are passive dispersers and therefore have little control over their movement relative to prevailing water currents (Bowman et al., 2018). Physical constraints—specifically, thermal conditions and water currents—and competition can be assumed to be the most important factors determining relative abundances of the two species in this system. Thus, we used thermal conditions, water currents, and competition to construct a model with an assumption that predation pressure and habitat availability would impact species evenly. For this model, vertical water flow and average temperatures of the entire water column are used as conservative estimates for realized habitats in order to partially account for differences due to depth. Thus, depth is not modeled explicitly but accounted for without overcomplicating the model.

To account for variation in thermal conditions, dispersal, and competitive dynamics, we developed a metacommunity model in which resident and invader dynamics are governed by a modified Lotka-Volterra system:

$$\frac{dR_i}{dt} = r_R(T)R_i \left( \frac{K_i - R_i - \alpha I_i}{K_i} \right) + \sum_{x \in j,k} m_x R_x - \sum_{y \in j,k} m_y R_i \quad (1)$$

$$\frac{dI_i}{dt} = r_I(T)I_i \left( \frac{K_i - I_i - \beta R_i}{K_i} \right) + \sum_{x \in j,k} m_x I_x - \sum_{y \in j,k} m_y I_i, \quad (2)$$

where  $dR/dt$ ,  $dI/dt$  are the rates of change in abundance of resident ( $R$ ) and invader ( $I$ ) species (*E. baikalensis* and *D. longispina*, respectively) in focal patch ( $i$ ),  $r$  is temperature ( $T$ )-dependent intrinsic growth rate taken from thermal performance curves (TPCs), and  $K$  is the carrying capacity of the focal patch ( $i$ ). Dispersal ( $m$ ) occurs in both directions along a linear chain of

patches situated from the innermost point in Chivyrkuy Bay to the open lake (Figures 1, 2A).

Dispersal includes emigration (immigration) from (to) the focal patch to (from) the immediately preceding bayward patch ( $j$ ) and immediately succeeding lakeward patch ( $k$ ). Competition

parameters represent the influence that *Epischurella* has on *Daphnia* ( $\alpha$ ) abundance and *Daphnia* has on *Epischurella* ( $\beta$ ) abundance.

## Model Parameters

### Thermal Performance Curves

Intrinsic growth rates ( $r$ ) follow left-skewed curves for thermal performance (Amarasekare and Savage, 2011) parameterized specifically for each zooplankter (Figure 3). These thermal performance curves (TPCs) are constructed from three parameters: fecundity ( $\bar{b}(T)$ ), development ( $\alpha(T)$ ), and mortality (juvenile  $\bar{d}(T)$  and adult  $d(T)$ ), measured across a range of different temperatures. We estimated these parameters for *Epischurella baikalensis* from experiments (Ozersky et al., 2019) and from the literature for *Daphnia longispina* (Bowman 2019). The TPCs account for metabolic instabilities at higher temperatures and incorporate differential effects on development and fecundity (Amarasekare and Savage, 2011, eq. 11):

$$r_m = -d_{T_R} \exp(A_d TD) + \frac{l}{\alpha_{T_R} \exp(A_d TD)} \times W \left( \bar{b}_{T_R} \alpha_{T_R} \exp \left\{ A_\alpha TD - \left[ \frac{(T - T_{opt_b})^2}{2s^2} \right] \right\} + \alpha_{T_R} \exp(A_\alpha TD) [d_{T_R} \exp(A_d TD) - \bar{d}_{T_R} \exp(A_{\bar{d}} TD)] \right), \quad (3)$$



where  $m$  is the species of interest.  $A$  is the Arrhenius constant for mortality at adult ( $d$ ) and juvenile ( $\bar{d}$ ) stages.  $T_R$  is a reference temperature (in K) as compared to  $T_{opt}$ , the temperature (in K) where fecundity is maximized, and the variability around that optimum is defined by  $s$ . The temperature differential ( $TD$ ) is defined as  $TD = [(1/T_R) - (1/T)]$ . The terms in equation (3) represent the effects of temperature on the three parameters that make up its calculation: 1) The first term corresponds to the effect of temperature on adult mortality; 2) the second term product  $\log$  corresponds to the effects of temperature on development, fecundity, and their interactions by using exponential, Gaussian, and Gompertz-like functions, respectively. For a more in-depth explanation of the behavior of these TPCs, see (Amarasekare and Savage 2011).

### Competition Parameters

We used competition parameters established in the literature for *Daphnia* spp. competing against conspecific populations with little genetic diversity and high genetic diversity as the most conservative estimate for our model (Tagg et al., 2005). *Daphnia* exhibit strong intraspecific competitive effects (Hu and Tessier, 1995; Cáceres, 1998; Johnson and Havel, 2001) and Allee effects (Hanski and Ranta, 1983; Kramer and Drake, 2010). Thus, for the competitive effect of the resident *Epischurella* on *Daphnia* ( $\alpha=0.896$ ), we conservatively estimate this to be proportional to the competition between two *Daphnia* populations with higher genetic diversity, i.e., low competition (Table 1). Whereas, we estimate the competition effect of *Daphnia* on *Epischurella* ( $\beta=1.01$ ) to be higher (Richman and Dodson, 1983)—proportional to that of *Daphnia* conspecific competition with low genetic diversity, i.e. high competition (Tagg et al., 2005); we additionally tested a range of alpha and beta values via sensitivity analysis.

## Dispersal and Water Current Parameters

Though zooplankton have surprisingly fast swim speeds, sometimes reaching 0.30 m/s (Bradley et al., 2012), they are generally thought to be controlled by the currents of the water columns in which they inhabit (Folt and Burns, 1999). Especially in large lakes, such as Lake Baikal, where surface currents and steady wind patterns create seasonally strong currents (Weiss et al., 1991; Wüest et al., 2005; Kirillin et al., 2012; Troitskaya et al., 2015), we expect zooplankton to be especially limited by the prevailing currents (Bowman et al., 2018). Nevertheless, to explore any possibilities of powered dispersal, swimming speeds were estimated from the literature at 0.0074 m/s for *Daphnia* species (Jacobs 1968) and 0.0030 m/s for copepod species (Bradley et al., 2012).

The surface currents of Lake Baikal have been estimated at an average of 0.09 m/s (Schmid et al., 2008). Note that surface currents are nearly an order of magnitude higher than average zooplankton swim speed. Given that the depth of Chivyrkuy Bay is on average between 20-30m and that surface currents decay with depth predictably (approximately exponentially) (Ekman, 1905), we used the Ekman motion equation (Ekman, 1905) to estimate the average horizontal velocity of a parcel of water in the Ekman layer (upper 30m) of the water column:

$$V_E = -\frac{\tau^y}{\rho f}; U_E = -\frac{\tau^x}{\rho f} \quad (4)$$

where  $V$  and  $U$  are the directional velocities in the  $x$  and  $y$  directions, respectively and where  $\tau$  is the wind stress. In the Ekman equation,  $\rho$  is density, and  $f$  is the Coriolis parameter, both of

which are assumed to be constant in the Lake Baikal system, making Ekman velocity in any direction directly proportional to the wind stress, i.e., max surface currents (0.9 m/s).

Initial conditions: invasion and mortality rates

Following methods from Hanski et al. (2000), we set the initial invasion rate in the most bayward patch an order of magnitude lower (equal to 0.001 individuals per timestep) than the global mortality rate (equal to 0.01 individuals per timestep).

Field Data

Field Samples

All zooplankton samples were collected in Summer 2013 during the day with a 50 cm diameter, 100  $\mu$ m mesh plankton net. Samples were taken from 100 m to 0 m at stations where depth was >100 m and from max depth to 0 m where depth was <100 m. Samples were condensed and stored in 70% ethanol and refrigerated until counting. On three separate traverses (independent replicates) of Chivyrkuy Bay, we collected samples along a transect of the 109 meridian East, spanning from 125m or greater depth in open Baikal to the inner bay (Figure 1). We collected abiotic environmental data concurrently with zooplankton sampling. Data for temperature, dissolved oxygen, surface temperature, and chlorophyll concentrations were collected using a YSI Sonde and averaged across the water column for each of the transect samples (Figure 4 and Electronic Supplementary Material (ESM) Figure S1).

## Analysis

We analyzed five different modified Lotka-Volterra models (Eq. 1 and 2) for their predictive power for the field data we collected: 1) temperature only; 2) temperature + competition; 3) temperature + dispersal; 4) temperature + competition + dispersal; and 5) temperature + high dispersal (Table 2). The temperature-only model accounts for the differential intrinsic population growth rate of the two species given the temperature in a patch by setting the competition coefficients to zero and zeroing dispersal. The competition and temperature model incorporates the competition coefficients and eliminates the dispersal between patches (Equations 1, 2). The dispersal and temperature model eliminates competition and incorporates dispersal between patches. The temperature, competition, and dispersal combined model accounts for both competitive effects between the species and the ability to disperse to different patches entrained with moving water masses. We also created a temperature and high-dispersal model in which we increased the dispersal between all patches to equal the maximum surface current strength ( $0.09 \text{ m s}^{-1}$ ) calculated in Lake Baikal (Schmid et al., 2008) to represent a highly-mixed system.

We calculated the relative species abundances for each patch for all models after  $10^6$  timesteps, at which point all models tested here converge on equilibria for each patch. We then compared the relative abundances predicted by each model for each patch to the field data collected in summer 2013. All model calculations were performed in Mathematica (Wolfram Research, 2018).

## Model Selection and Sensitivity Analysis

We used a maximum likelihood approach for model selection comparing our model predictions to our observed relative abundances and then comparing model  $AIC_c$  values to select the optimum model(s) (Bolker, 2008, Table 2). We performed model selection using the `bbmle` package (Bolker, 2017) in R with a normal distribution.

We completed a sensitivity analysis on the set of models using the R package “ODESensitivity” (version 1.1.2) incorporating a global Morris screening for ordinary differential equations. To test the relative influences of each parameter within the model, this approach uses a stepwise method to probe parameter space within defined ranges that are broader than is biologically relevant for each parameter (e.g., 0.1% to 100% emigration rate, 0.01-0.30 intrinsic rates of increase, etc.).

### Climate Change Projections

After model selection, we analyzed the optimum model (temperature and dispersal) for future projections given estimated climate change data for the region (Moore et al., 2009). From long-term IPCC datasets of global surface waters (0-100 m), Moore et al. (2009) estimated that the upper waters (0-100 m) of Lake Baikal will undergo mean annual temperature increases of 2.7-6.4°C (0.039 – 0.091°C/yr) in the next 60-80 years. We estimated the relative abundances at equilibrium of these two zooplankton species in Lake Baikal given these projected temperature changes for this same time period (+0.061°C/yr for 70 years) and explore how future increases in temperature may affect the relative species abundances.

## Results

### Empirical Results

From field sampling in 2013, we found that as Chivyrkuy Bay becomes shallower in its inner reaches, average water column temperatures approach 20°C (P6) compared to the 5°C in the open lake (P1) (Figure 4). We found that relative abundances of these two zooplankters ranged from zero percent *D. longispina* in the assemblage in the open lake (P1) to 100 percent *D. longispina* in the assemblage in the inner reaches of Chivyrkuy Bay (P6) (Figure 2A-B). We found that levels of dissolved oxygen and chlorophyll showed no trend across the patches (ESM Figure S1). We found no east-to-west trends in abundance, but absolute densities of zooplankton decreased dramatically from nearly 1000 individuals/m<sup>3</sup> in the offshore sample (>99.9% *Epischurella baikalensis*) to 100 individuals/m<sup>3</sup> (100% *Daphnia longispina*) in the inshore samples.

### Thermal Performance Curves

We observed several distinct outcomes from modeling the thermal performance of *Epischurella baikalensis* and *Daphnia longispina* in the Lake Baikal system. Interestingly, the TPC for *E. baikalensis*, the endemic, stenothermic copepod, was notably not as left-skewed as is typically expected (Figure 3). Even in the warmer temperatures of Chivyrkuy Bay, *E. baikalensis* had positive growth rates across all temperatures, though samples from the Chivyrkuy Bay's interior are near the thermal maximum for positive per capita growth (Figure 3).

We estimated that *Epischurella baikalensis* had a much narrower thermal environment where its growth rate is positive (0-25°C) than *Daphnia longispina* (2.5-35°C). *Epischurella baikalensis*'s thermal optimum was at 9°C, and *D. longispina*'s was at 21°C. The large difference in these thermal optima further illustrates the physiological limitations on *D. longispina* in a very cold lake and *E. baikalensis* in a warming bay. According to our analyses, *D. longispina* also has a higher maximum population growth rate (0.28) than *E. baikalensis* (0.22), highlighting the species' different reproductive strategies (Hebert, 1981; Bowman et al., 2017).

We found that *Daphnia longispina* has a much wider thermal tolerance with a maximum at 22°C (Figure 3) that encompasses all temperatures currently observed in Baikal and many higher temperatures currently outside the thermal range of Baikal (Timoshkin et al., 2016). We used a worldwide parameterization for *Daphnia longispina* rather than a Baikal-specific analysis to account for potential effects in the TPC that may be unapparent under current conditions of Baikal. *Daphnia* have the potential to rapidly evolve thermal tolerance (Geerts et al., 2015), so we chose to include the broadest sampling possible to capture any future adaptive ability of *D. longispina*.

#### Current conditions and model selection

We found that most empirical samples were dominated by either *E. baikalensis* or *D. longispina*. A portion of the zooplankton assemblage was also made up of *Cyclops kolensis*, ranging from 0-24% of the assemblage. In this model, we assume the predation pressure of *Cyclops kolensis* to be minimal and equal on both *E. baikalensis* and *D. longispina* in most years, so we did not explicitly incorporate it into our models. Although *C. kolensis* is always present in

the water column, occasionally, its annual abundance reaches 57 g m<sup>2</sup> but also has been found to be as low as 0.01 g m<sup>2</sup> (Zaidykov et al., 2020). Future work should explore how differences in predation pressure, especially in high abundance years and by other piscivorous fishes, may affect *E. baikalensis* and the interactions between *E. baikalensis* and *D. longispina*.

Temperature increased as Chivyrkuy Bay became shallower, but this corresponded to no discernible patterns in chlorophyll or dissolved oxygen (Figure S1). Interestingly, we found no relationship with dissolved oxygen (Figure S1) except at roughly thermocline depth in Patch 3, likely due to internal shear mixing. The effects of chlorophyll and dissolved oxygen on zooplankton has been explored in other areas (Hampton et al., 2008), and thus, were not explicitly carried into our models.

After model parameterization (Table 1), we ran each of our five models and compared the predicted species assemblages to those collected in the field. We found that the temperature and dispersal model best fit the current assemblage data (Figure 2B) and resulted in the lowest AIC<sub>c</sub> score among all five models tested (Figure 2C, Table 2). This model specifically accounted for the differences in per capita growth rates experienced by the two zooplankters and accounted for their passive and active dispersal into different areas in the lake and bay. We found that models including competition were substantially weaker than models that only accounted for per capita growth rate differentials ( $\Delta\text{AIC}_c=6.9; 6.9$ ) (Table 2). All models, except for the temperature and high dispersal model ( $\Delta\text{AIC}_c=7.7$ ), were able to recapitulate the empirical findings that open lake patches were dominated by *E. baikalensis*, and that bay patches were dominated by *D. longispina*. The assemblage results for all other models can be found in the supplement (Figure S2).



The sensitivity analysis revealed that the most sensitive parameters in the model set are the intrinsic rates of increase ( $r$ ) for each species, followed by and, to a lesser degree, dispersal parameters, and then carrying capacity (Supplemental Figure S3). Our model is most sensitive to the parameters we are intentionally testing and less sensitive to the initial conditions, global mortality rates, or competition parameters. Relatively low contributions from all parameters reflects robustness in this model set.

### Future Temperature Projections

Given the predicted thermal increases for Lake Baikal in the coming 60-80 years (Moore et al., 2009), we used the temperature and dispersal model to determine the effects of the minimum, median, and maximum predicted changes in temperature at equilibrium (Figure 5). We found that at the median predicted increase in temperature ( $\Delta T = 4.3^\circ\text{C}$ ;  $0.061^\circ\text{C}/\text{yr}$ , 70 yrs), the main lake basin began to experience noticeable abundance of *D. longispina*. At the maximum predicted increase in temperature ( $\Delta T = 6.4^\circ\text{C}$ ;  $0.091^\circ\text{C}/\text{yr}$ , 70 yrs), over 40% of the species assemblage in the open lake patch was composed of *D. longispina*.

[Insert Figure 5 about here.]

### Discussion

Biological invasions are increasing in magnitude and frequency due, in part, to global change (Dukes and Mooney 1999), and these invasions may drastically affect fragile ecosystems (Nilsson and Grelsson 1995). In aquatic systems, where endemic species, such as *Epischurella*

*baikalensis*, cannot readily migrate to a new habitat, evolution and local adaptation are limited ways of escaping competition and changing environments (Shurin and Havel 2002). We found that temperature and dispersal limitation best predict *Daphnia longispina* current distribution, preventing establishment in the main basin of Lake Baikal. However, in our analyses, future warming may reverse this effect, possibly within the next century. Under present conditions, *D. longispina* is spatially-limited to Baikal's periphery of shallow bays (Hampton et al., 2008), and *E. baikalensis* exhibits thermal plasticity and local adaptation (Bowman et al., 2018), yet the interaction between rising water temperatures and dispersal may mitigate these buffers. We demonstrate here an important example of a synergy between temperature and dispersal as a catalyst for broadening species distributions and increasing invasion probability.

#### Future Scenarios and Thermal Performance

We found that under the present predictions for temperature increases in Lake Baikal, *D. longispina*'s range is modeled to increase to the entire lake and no longer be contained in Chivyrkuy Bay. Though its presence has been noted for >50 years, few *D. longispina* are ever recovered outside of Chivyrkuy Bay or other shallow bays (Sheveleva et al. 1995). However, the temperature and dispersal model predicts that dispersal out of Chivyrkuy Bay combined with the thermal differential of the open lake does not allow *D. longispina* to establish in the main basin. As temperature increases in the lake, the predicted outcomes show that *D. longispina* becomes more and more likely to dominate patches previously dominated by *E. baikalensis*. Moreover, we found from modeling the TPCs of both species that as Baikal's temperature increases, decreases in *E. baikalensis*'s intrinsic rate of increase became particularly pronounced while *D. longispina*

approached its thermal optimum. This suggests that *D. longispina* will not only disperse into but thrive in the main basin as temperature increases reach its thermal optimum.

We predicted the magnitude of temperature change necessary for *D. longispina* to reach majority, becoming the dominant species of the assemblage in the open lake patch ( $\Delta T = 7.6^{\circ}\text{C}$ ). This would require the average temperature of Lake Baikal's upper 100m to warm  $7.6^{\circ}\text{C}$ . The current maximum prediction for the next 60-80 years is  $6.4^{\circ}\text{C}$ , suggesting that in the next century and a half, Lake Baikal will likely be near or reach these average temperatures of the top 100m favoring the expansion of *D. longispina* on a whole-lake scale. We also estimated that the relative abundance of *D. longispina* reaches 100% at  $\Delta T = 8.0^{\circ}\text{C}$ , highlighting *D. longispina*'s critical advantage over *E. baikalensis* at higher temperatures.

Understanding the limited thermal range in which *E. baikalensis* has a sustainable positive per capita growth rate is important for its success in a changing thermal environment. This cold-adapted stenotherm has a per capita growth rate maximum at  $9^{\circ}\text{C}$  (Figure 3). Given the projected warming of the Lake Baikal system (Moore et al., 2009), *E. baikalensis* will face much higher water temperatures in the near future. However, *E. baikalensis* may have behavioral adaptations for mitigating higher temperatures. For example, *E. baikalensis* is found from surface to maximum depth across Baikal (Afanasyeva, 1998), implying that behavioral thermal regulation may occur to evade higher surface temperatures or that reproductive strategies may change to weather non-benign conditions (Bowman et al., 2017). Even in a warming environment, *E. baikalensis* will have access to cooler temperatures beneath the thermocline. Moreover, recent work has revealed signals of local adaptation related to thermal tolerance genes, especially prevalent in warmer areas of Baikal (Bowman et al., 2018).

In the environments where *D. longispina* is most successful, like Chivyrkuy Bay, most patches are not near *D. longispina*'s thermal optimum (Figure 3), suggesting that with continued warming, *D. longispina* may continue to become more and more successful at dominating warmer waters. Therefore, *E. baikalensis* may be forced to migrate near or below the thermocline to achieve a more favorable thermal environment particularly in areas where surface waters reach much higher temperatures as in Chivyrkuy Bay and Maloe More (Bowman et al., 2018). In the main basin, though *D. longispina* could dominate the upper 100 m of Baikal, *E. baikalensis* will likely maintain thermal advantage below the thermocline where Lake Baikal remains relatively stable at ~4°C (Izmest'eva et al., 2016). Our models also do not explore the use of deeper thermal refugia for *E. baikalensis*, but this would, of course, introduce other pressures limiting the success of *E. baikalensis*, such as resource availability and predator avoidance near the bottom of the photic zone. Though much work has been done on the thermal processes that govern the water exchange in Lake Baikal (Weiss et al. 1991; Schmid et al., 2008), it remains unclear how large increases in the temperature of the surface waters will affect mixing below the thermocline and whether that may affect this theoretical thermal refugia for *E. baikalensis* (Schmid et al., 2008).

A caveat of the models is not incorporating evolution or local adaptation to a changing thermal environment over time. However, given *D. longispina*'s proclivity for higher temperatures coupled with its much shorter generation time and ability to reproduce sexually and via cyclical parthenogenesis (Hebert 1981), incorporating evolution into the models would likely only increase the strength of or shorten the time until whole-lake expansion. But, given its particular reproductive cycle, it is unclear how *D. longispina* populations will fair in the main basin. *Daphnia* spp. create resting eggs (ephippia) in late Fall which are then released and hatch

from the sediment in the following Spring, creating the next generation of *Daphnia* (Hebert, 1981). However, the main basin of Lake Baikal is incredibly deep (~1500m), making the success of this reproductive strategy unlikely given the need for particular environmental cues for resting eggs to hatch (Carvalho and Wolf 1989; De Meester and De Jager 1993; Lass et al., 2005). If these resting eggs are not viable in the main basin and *D. longispina* is unable to sustain a population over winter (e.g., like *E. baikalensis* (Ermakov, 2011), this may further limit the expansion of *D. longispina* into the main basin.

*Daphnia* in the nearshore and bays of Lake Baikal consistently produce protective spines in response to predation pressure, which is seen less often in the offshore environment (Korzun and Pitulko, 2010). Although it is not known whether there are major phenological difference between inshore and offshore *Daphnia*, individuals in bays and inshore environments develop spines earlier in development and have spines more often (Korzun and Pitulko, 2010), suggesting that more resources are devoted to predator avoidance in inshore regions like Chivyrkuy Bay. Although it remains unclear whether *Daphnia* in inshore regions have source-sink dynamics with offshore populations, it is plausible that inshore populations may have longer growing seasons, increasing momentum for offshore dispersal.

Another important distinction for this model is the use of relative abundance versus biomass. Although *D. longispina* and *E. baikalensis* are relatively similar in size (1-2mm), each offers a different nutrient composition indicative of their life histories (Bowman et al., 2017). For example, *E. baikalensis* are likely to be more lipid-rich and offer a higher quality food source for higher trophic levels, whereas *D. longispina* are more likely to reflect immediate environmental nutritional conditions (Bowman et al., 2017). Because of their similarity in size, relative abundance is likely a good indicator of biomass, but in order to understand the impacts of a *D.*

*longispina* expansion on energy flow to higher trophic levels including sight predators like the endemic golomyankas, the interplay between biomass and abundance should be explored. For example, an increase in abundance of *D. longispina* may not directly correlate to a loss in *E. baikalensis* biomass as mitigated by top-down predation from oilfishes.

In addition to top-down effects, both species may compete directly for available resources, e.g., phytoplankton. The competitive effects of *D. longispina* on *E. baikalensis* may be overestimated; it has been shown that *E. baikalensis* has evolved special mandibles unlike others in its sister genera for the specific purpose of crushing the endemic diatoms that occur in Baikal (Bowman et al., 2019). However, in Chivrykuy Bay and other warm areas of the lake, warm water phytoplankton species are also becoming increasingly common (Hampton et al., 2014). Thus, the outcomes of bottom-up controls on the system may be limited or further advantage *D. longispina* as Baikal continues to warm and green, filamentous algae become more common (Ozersky et al., 2018).

It is worth noting that recent work suggests the subsistence of *Daphnia* spp. populations throughout the winter (de Senerpont Domis, L N et al., 2007; Lampert et al., 2010; Hamrová et al., 2011), which then produces significant priority effects in the subsequent Spring assemblage (Hanski and Ranta, 1983; De Meester et al., 2002; Louette and De Meester, 2007) further advantaging *D. longispina*. And yet another possibility is that *D. longispina* shows variation in ephippia either sinking to the bottom (not viable in Baikal due to its depth) or floating on the surface (Ślusarczyk et al., 2017), potentially overwintering immediately under ice. Future work should explore *D. longispina*'s under-ice ecology in other Holarctic systems (Hampton et al., 2017) to better understand how *D. longispina* may perform in the over six-month ice-on period experienced in Lake Baikal (Hampton et al., 2008). Ephippia could be transported offshore

during upwelling events, leading to local, high-density patches of *D. longispina* that may not be able to reproduce as the water masses cool (Megard et al., 2003). The meso-oceanic properties of great lakes may further complicate *D. longispina*'s ability to appear offshore via surface seiches or remain inshore via coastally trapped waves (Sterner et al., 2017). Future work should consider physical processes that may explain spatial distribution and variability of high-density zooplankton patches that may be the result of meso-oceanic processes, unique to great lakes and Baikal.

Although it has a remarkably species-depauperate zooplankton assemblage being dominated year-round by a single calanoid copepod species, Lake Baikal will likely be subject to trends as seen in the Laurentian Great Lakes, where cladoceran abundance is highly correlated to chlorophyll abundance and smaller-bodied zooplankton are replaced by larger-bodied zooplankton due to decreases in vertebrate predation and increases in invertebrate predation (Barbiero et al., 2019; Brown and Branstrator, 2004). In the Laurentian Great Lakes, there are seasonal trends in spatial structure where Spring assemblages are more homogenous than in Fall (Watson and Wilson, 1978). Cladocerans and other warm-water species have been shown to contribute less to offshore biomass than cold-water species like *Epischura* and *Epischurella* (Pawlowski et al., 2018); however, generally, *Daphnia* contribute substantially to offshore biomass interannual variation (Pothoven and Fahnensteil, 2015). If Baikal trends follow other Great Lakes, there are likely to be bottom-up (more abundant, warm-water green algae) and top-down (less piscivorous and more invertebrate predation) effects that promote more variable offshore assemblages. Baikal's future zooplankton assemblage may more closely resemble that of the Laurentian Great Lakes and become more seasonally and interannually variable if

warming trends continue, which may have far-reaching repercussions for species adapted to an historically stable zooplankton community.

In aquatic systems, horizontal mixing has largely been discounted either by the assumption that lakes are fully-mixed, closed systems (Vollenweider, 1975; Huisman and Weissing, 1994; Goyette et al., 2000; Mironov et al., 2010) or by assuming that the horizontal distribution of zooplankton is roughly uniform (Stockwell et al., 2002). Here, we show that those assumptions predicted our species assemblages especially poorly (ESM Figure S2,  $\Delta AIC_c=7.7$ ). When attempting to predict species' range projections for inland waters, we should also be accounting for the physical properties of horizontal mixing and its interaction with biotic and abiotic factors like competition and temperature. For example, the *D. longispina* population resident to Chivyrkuy Bay has been relatively localized to a single bay for ~50 years (Sheveleva et al., 1995), which ultimately could lead to incorrect assumptions about its threat to the ecosystem under different environmental regimes. Our results suggest that dispersal limitation and temperature, currently and in the immediate future, could mediate the effects of this non-native. It remains unclear how to limit zooplankton dispersal in practice except to control any continued human-mediated dispersal, such as boat traffic (Shurin and Havel, 2002). More importantly, we determined that future warming may reverse the containment of a non-native species, possibly enhancing a lake-wide range expansion within the next century and threatening the persistence of locally adapted endemics and changing ecosystem function.

Here we demonstrated two major findings: 1) dispersal and temperature are major factors in limiting non-native expansion in large lake systems, despite a perceived lack of physical barriers and 2) current barriers to expansion may be reversed in the future due to synergy with increasing temperature. This case study in Lake Baikal highlights the need to explore these



synergistic interactions between dispersal and temperature in aquatic systems. As we try to understand and predict the complexity of how global change will affect species interactions, we must consider the interactive effects of physiology and movement—in our models both must be incorporated to accurately estimate empirical observations.

This synergy between temperature and dispersal may be present in other ecosystems but remain undetected under present conditions. Ecosystems that contain low species diversity (Dukes, 2002; Stachowicz and Byrnes, 2006) or many endemic species are of particular risk of invasion (Thomson, 2005; Riley et al., 2008), and understanding how invasion and climate change interact under different environments enables us to manage and predict future changes in these systems.

### **Acknowledgements:**

We would like to thank our three reviewers for their helpful and insightful comments that greatly improved the manuscript. We are grateful to the Lake Baikal Dimensions of Biodiversity consortium members, the crews of research vessels *Professor Treskov* and *Professor Kozhov*, and to the faculty and staff of Irkutsk State University Bolshie Koty field station for assistance with sample collection. We are grateful to Ted Ozersky and Paul Wilburn for assistance with field work and Colin Kremer, Ted Ozersky, and Carla Staver for useful suggestions on earlier drafts of the manuscript. This work was supported by US National Science Foundation grants DEB-1136710 to LYY and DEB-1403550 to DJW.

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Table 1. Estimated values for model parameters and their original sources. Mortality and invasion values are rates per timestep in the model. Invasion rate appears in the initial timestep only.

<b>Model Parameter</b>	<b>Estimate</b>	<b>Source</b>
Baikal surface current	0.09 m/s	Schmid et al., 2008
High dispersal value	0.90 m/s	Modified from Schmid et al., 2008
<i>Daphnia</i> swim speed	0.0074 m/s	Jacobs, 1968
Copepod swim speed	0.030 m/s	Bradley et al., 2012
Competition coefficient ( <i>Daphnia</i> on <i>Epischurella</i> )	1.01	Richman and Dodson, 1983
Competition coefficient ( <i>Epischurella</i> on <i>Daphnia</i> )	0.896	Richman and Dodson, 1983
Mortality Rate	0.01	Hanski et al., 2000
Invasion Rate (Initial)	0.001	Hanski et al., 2000
Thermal Performance Curves	See Below	Ozersky et al., 2019; Bowman, 2019

<b>Life History Trait</b>	<b>Species</b>	
	<i>Epischurella baikalensis</i> <sup>*</sup>	<i>Daphnia longispina</i> <sup>†</sup>
Fecundity ( $\bar{b}(T)$ ): $T_{opt_{\bar{b}}}$ (°K)	284.24	292.03
<i>s</i>	5.25	5.38
Development ( $\alpha(T)$ ): $A_{\alpha}$	-592.51	-3971.84
Juvenile mortality ( $\bar{d}(T)$ ): $A_{\bar{d}}$	$3.19 \times 10^{-7}$	$3.12 \times 10^{-7}$
Adult mortality ( $d(T)$ ): $A_d$	$3.47 \times 10^{-22}$	$5.29 \times 10^{-8}$

Table 2. Maximum likelihood model selection results for each of the five models when compared to a normal ( $N$ ) distribution. The Temperature + Dispersal model performed best.  $\Delta\text{AIC}_c$  values reflect correction for small sample sizes.

<b>Model</b>	<b><math>\Delta\text{AIC}_c</math></b>
	$X \sim N(\mu, \sigma^2)$
Temperature + Dispersal	0.0
Temperature Only	4.5
Temperature + Competition + Dispersal	6.9
Temperature + Competition	6.9
Temperature + High Dispersal	7.7



## List of Figure

Figure 1. Lake Baikal is located in Eastern Siberia, Russia, north of Mongolia. Chivyrkuy Bay is located in the Northern Basin. Transect sampling locales from July 2013 are colored in the inset by the model patches to which they correspond. Temperatures correspond to mean water column temperatures for each sample group.

Figure 2. The Chivyrkuy Bay (A) empirical sampling sites, (B) current species assemblages collected in July 2013, and (C) temperature + dispersal model predictions of species assemblages. A) Transect sampling was completed in July 2013, and each transect triplet was then modeled as a separate patch in our metacommunity model. B) Relative abundances of the two focal species: the endemic copepod, *Epischurella baikalensis* (blue), and the invader cladoceran, *Daphnia longispina* (orange) from empirical samples of Chivyrkuy Bay. C) Model predictions of the relative abundances of both focal species in the temperature + dispersal model. Temperatures correspond to mean water column temperatures for each triplicate sample.

Figure 3. Thermal Performance Curves (TPCs) for the endemic copepod, *Epischurella baikalensis* (blue), and the non-native cladoceran, *Daphnia longispina* (orange). The per capita growth rate ( $r$ ) across different temperatures are determined from Eq. 3, though note Eq. 3 uses temperatures in Kelvin which are converted, here, to Celsius. Vertical lines correspond to the mean temperatures of patches sampled in Chivyrkuy Bay in 2013 with P1 being the main lake basin and P6 being the most bayward patch (see Figure 2B).

Figure 4. (Left) Mean temperature of the 6 focal patches sampled in August 2013 in Chivyrkuy Bay. More northern latitudes (left-most X-values) represent the main lake basin, more southern latitudes represent sampling sites within Chivyrkuy Bay. ( $R^2=0.91$ ,  $P=0.0032$ ) (Right) Depth profile of Chivyrkuy Bay from sampling sites. Latitude same as Left with left-most values representing the main basin transition into the much shallower bay.

Figure 5. (Upper panel) Temperature projections from the optimal model (dispersal only). Relative species abundances of the endemic (blue) and invader (orange) zooplankters given a (A) 2.7C increase in mean patch temperature, the minimum predicted temperature increase, (B) 4.3C increase, the median predicted temperature increase, and (C) 6.4C increase, the maximum predicted temperature increase. Temperature increase predictions from Moore et al. (2009) for years 2080-2099. (Lower panel) Sub-optimal metapopulation model predictions of relative abundances of the endemic (blue) and invader (orange) zooplankters under current thermal environments. D) Temperature only model, E) Temperature+Competition only model, F) Temperature+Dispersal+Competition (full) model, G) Temperature + High Dispersal model. For more information about each model, see Methods and Model. For AICc values, see Table 2.

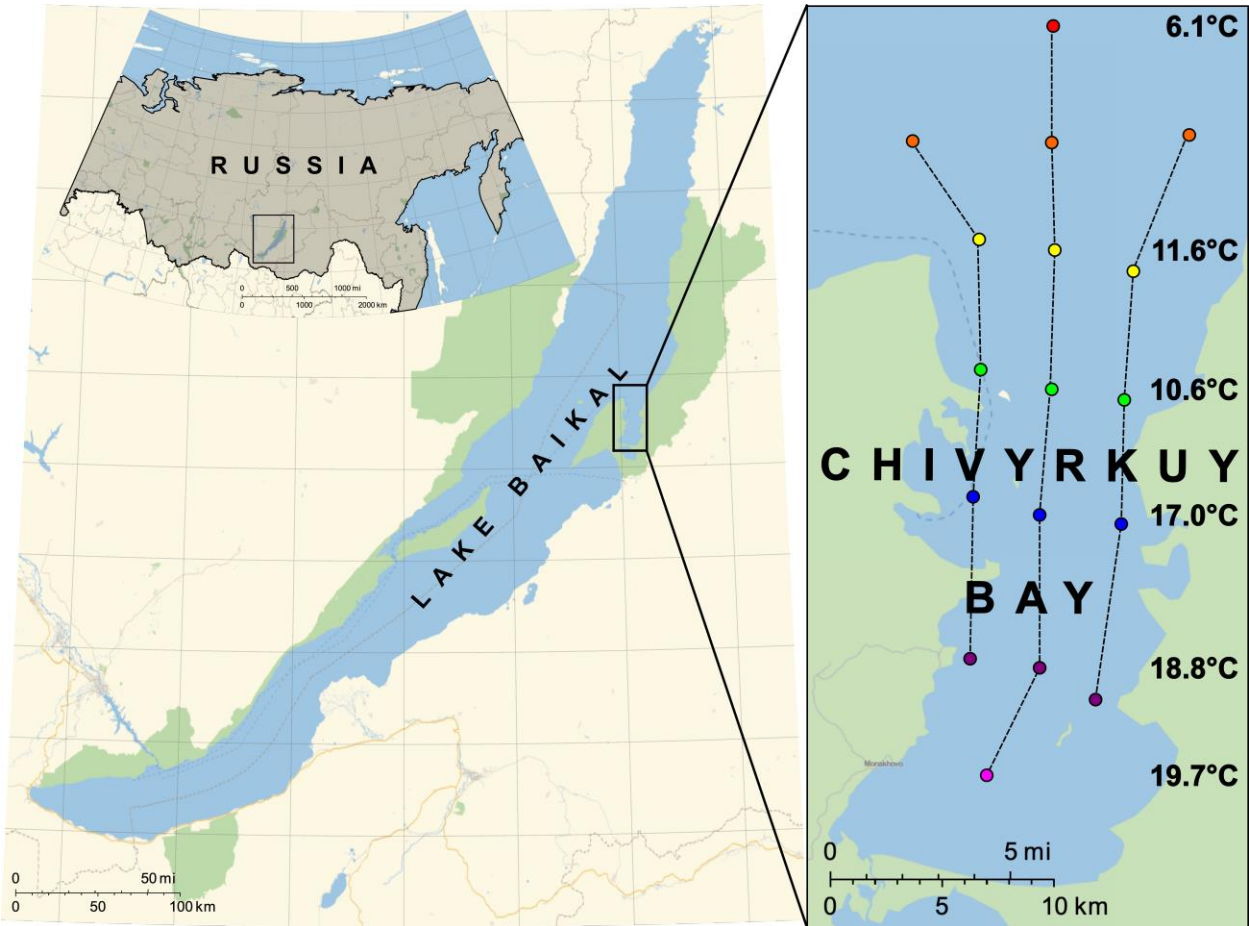


Figure 1.

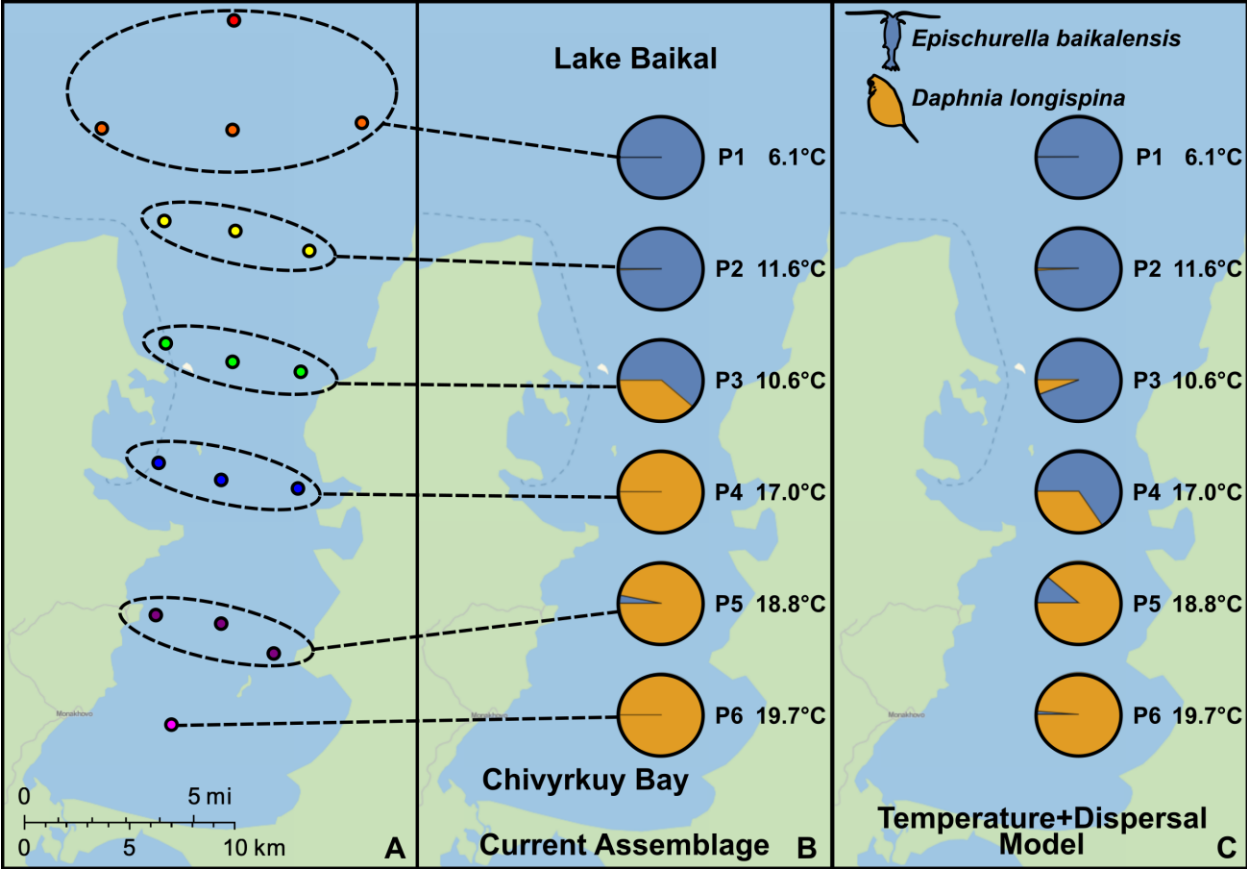


Figure 2.

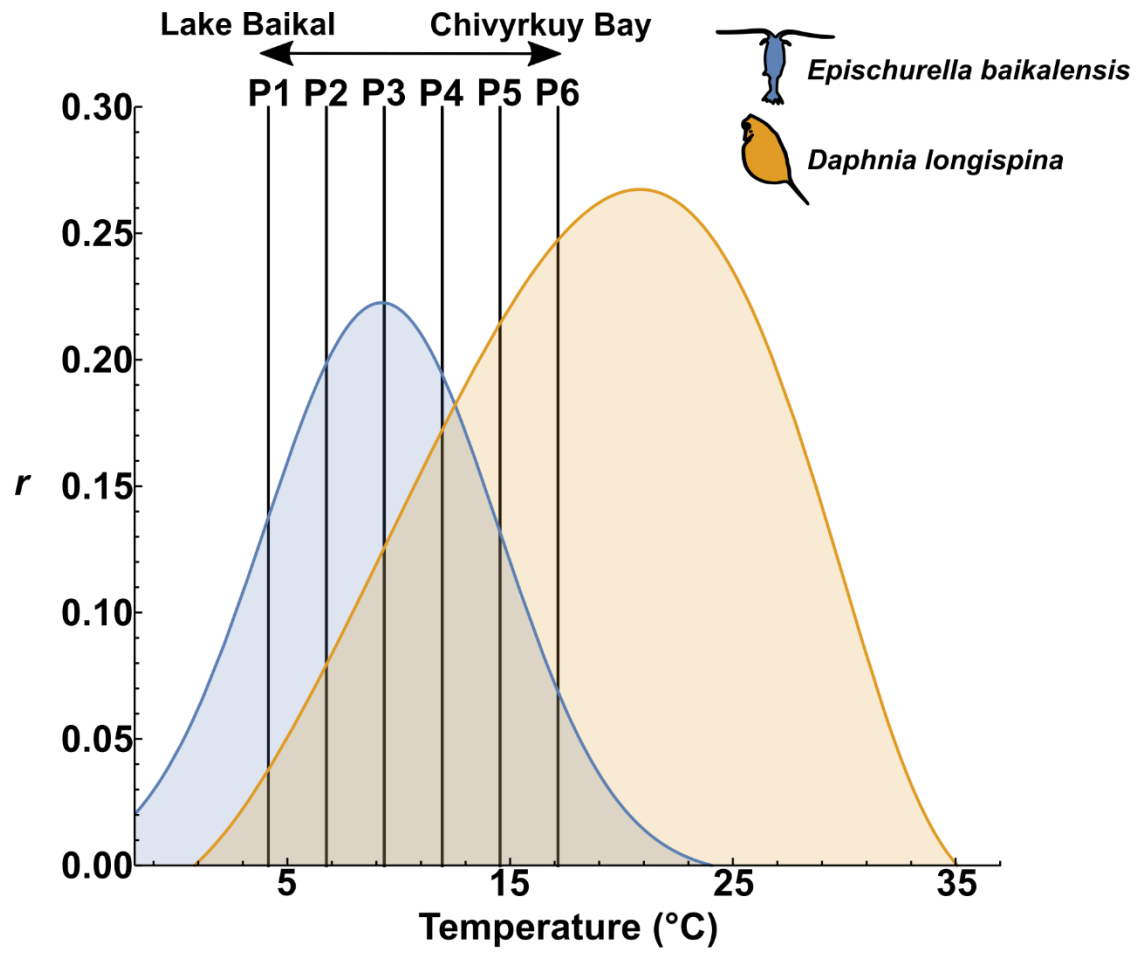


Figure 3.

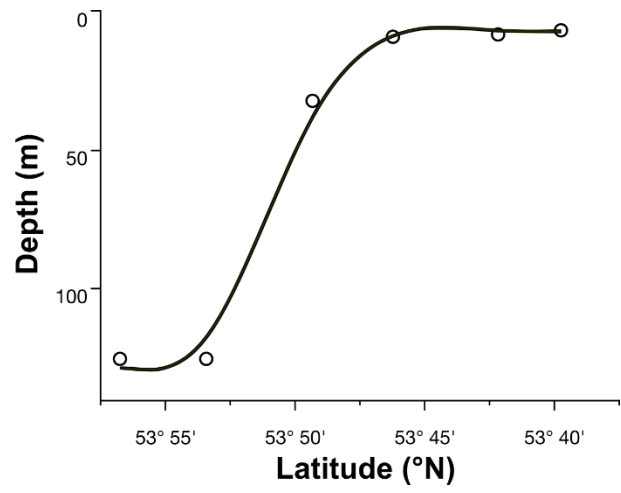
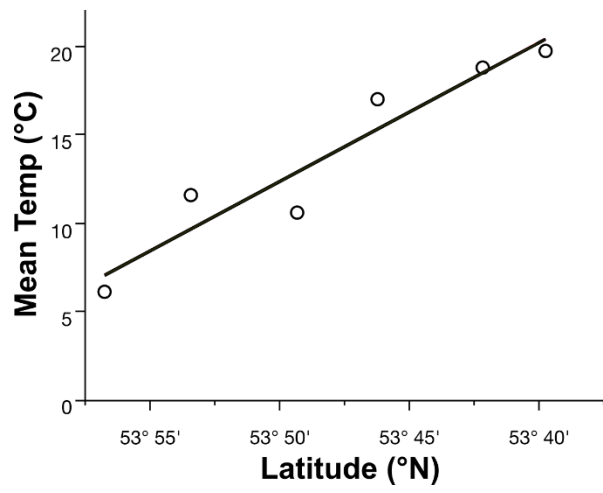


Figure 4.

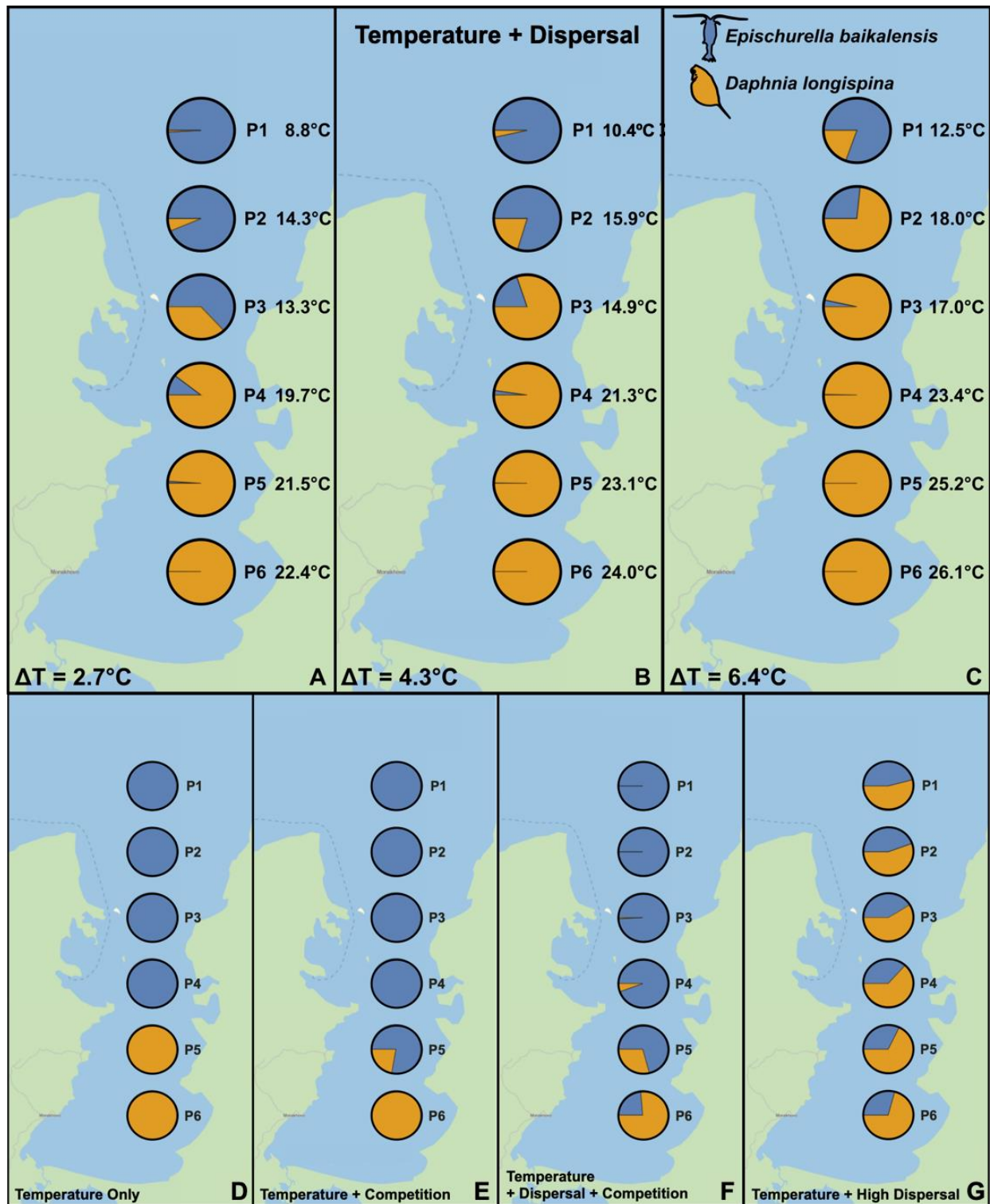


Figure 5.