Unexpected population response to increasing temperature in the context of a strong species interaction

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Abstract

Climate change is driving large changes in the spatial and temporal distributions of species, with significant consequences for individual populations. Community- and ecosystem-level implications of altered species distributions may be complex and challenging to anticipate due to the cascading effects of disrupted interactions among species, which may exhibit threshold responses to extreme climatic events. Toxic, bloom-forming cyanobacteria like *Microcystis* are expected to increase worldwide with climate change, due in part to their high temperature optima for growth. In addition, invasive zebra mussels (*Dreissena polymorpha*) have caused an increase in *Microcystis aeruginosa*, a species typically associated with eutrophication, in low-nutrient lakes. We conducted a 13-year study of a *M. aeruginosa* population in a low-nutrient lake invaded by zebra mussels. In 10 of the 13 years there was a significant positive relationship between *M. aeruginosa* biomass and accumulated degree days, which are projected to increase with climate change. In contrast, *Microcystis* biomass was up to an order of magnitude lower than predicted by the above relationship during the other three years, including the warmest in the dataset, following repeated heat-induced mass mortality of *D. polymorpha*. Thus, the positive relationship between *Microcystis* biomass and temperature was negated when its facilitating species was suppressed during a series of exceptionally warm summers. Predicting the net response of a species to climate change may therefore require, at minimum, quantification of responses of both the focal species and species that strongly interact with it over sufficiently long time periods to encompass the full range of climatic variability. Our results could not have been predicted from existing data on the short-term responses of these two interacting species to increased temperature.

Keywords

Species interactions, climate change, zebra mussels, harmful algae, *Microcystis*

Introduction

Anthropogenic climate change is causing rapid and large shifts in the environmental template of species and will increasingly do so in the future (IPCC 2014). Responses of individual species to recent climatic variation have already been documented, including range shifts (Perry et al. 2005, Chen et al. 2011), changes in the phenology of critical life history stages (Edwards and Richardson 2004), mass-mortality events and local extirpations (Garrabou et al. 2009, Smale and Wernberg 2013, White et al. 2015), and potentially extinctions (Pounds et al. 2006) across a broad range of taxonomic groups (protists, plants, invertebrates, vertebrates) and habitats (terrestrial, marine, freshwater). There is thus an urgent need for understanding and predicting the responses of species, as well as the resultant community- and ecosystem-level implications, to guide management and conservation decisions.

However, because species are embedded in communities composed of complex networks of interactions, the response of an individual species to a warming climate could result in complex cascading effects on ecosystems by modifying the predicted responses of other interacting species, possibly antagonistically (Suttle et al. 2007, Post and Pedersen 2008, Tylianakis et al. 2008, Van der Putten et al. 2010). The emphasis that has generally been placed to date on assessing the responses of individual species in isolation may therefore fail to accurately predict community- and ecosystem-level responses to climate change (Davis et al. 1998, Gilman et al. 2010). Information about how species interactions respond to climatic variation in natural systems, including anomalous climatic events, is currently limited (Jentsch et al. 2007, Gilman et al. 2010, Van der Putten et al. 2010).

Temperate freshwater lakes are experiencing rising water temperatures, longer growing seasons, and increases in the duration and stability of thermal stratification (Schindler et al. 1990, Winder and Schindler 2004, Jankowski et al. 2006, Austin and Colman 2008, Dobiesz and Lester 2009, Schneider and Hook 2010, Rösner et al. 2012), and all of these changes are expected to enhance the competitive success of planktonic cyanobacteria (Paerl and Huisman 2008, Paul 2008, Carey et al. 2012, Elliott 2012, Paerl and Paul 2012, Reichwaldt and Ghadouani 2012), a group that includes many harmful, bloom-forming species. Harmful cyanobacteria present substantial human health concerns and impair use of drinking and recreational waters (Carmichael 1994, Pilotto et al. 1997, Falconer 1999). Although there is a consensus that climate change will promote these nuisance phytoplankton in general, models that make predictions for specific harmful species are less developed (Pitcher 2012).

Furthermore and not surprisingly, attention has almost exclusively been focused on nutrient-polluted (eutrophic) lakes (Carey et al. 2008), since the biomass and relative abundance of harmful cyanobacteria generally increase with lake total phosphorus (TP) concentration (Smith 1985, Trimbee and Prepas 1987, Watson et al. 1997, Downing et al. 2001, Giani et al. 2005, Kotak and Zurawell 2007, Bigham et al. 2009). In contrast, invasion of low-nutrient lakes by the zebra mussel (*Dreissena polymorpha*) has resulted in significant biomass increases (3.6-fold in Michigan, USA) in *Microcystis aeruginosa*, a toxic, bloom-forming cyanobacterium typically indicative of eutrophic conditions (Vanderploeg et al. 2001, Raikow et al. 2004, Knoll et al. 2008, Sarnelle et al. 2010). Other species of bloom-forming cyanobacteria are generally either unaffected or decrease in the presence of *D. polymorpha* (Sarnelle et al. 2005, Sarnelle et al. 2012), potentially simplifying *in situ* investigation of climate effects on *Microcystis* in these socially and economically important ecosystems.

In low-nutrient Gull Lake (Michigan), where *Microcystis* promotion following zebra mussel invasion has been extensively studied (Sarnelle et al. 2005, Sarnelle et al. 2012), an unprecedented, heat-induced mass-mortality (~100%) of zebra mussels on epilimnetic substrata occurred in August of 2010. This mortality event was followed by two summers (2011-2012) of near-zero mussel densities, with limited recruitment until the summer of 2013 (White et al. 2015). The elevated temperatures, though lethal to *Dreissena*, are within the range of laboratory-derived optimal growth temperatures for *Microcystis* (~25-32 °C) (Zehnder and Gorham 1960, Robarts and Zohary 1987, Nalewajko and Murphy 2001, Imai et al. 2009). The difference in thermal tolerances between these two species may lead to complex responses of *Microcystis* to increasing temperatures in low-nutrient lakes, where *Dreissena* facilitates *Microcystis* success. *Microcystis* reaches detectable densities every summer and is the only toxin-producing cyanobacterium that regularly achieves high biomass in Gull Lake (Sarnelle et al. 2005), making this lake ideal for investigating the specific response of *Microcystis* to temperature variation in a long-term study.

Given the high temperature optima reported for *Microcystis,* which should lead to an increase in its competitive ability at elevated temperatures (McQueen and Lean 1987, Fujimoto et al. 1997, Kosten et al. 2012, Rigosi et al. 2014), we predicted that interannual variation in *Microcystis* biomass in Gull Lake should be positively influenced by water temperature. However, given that *D. polymorpha* is known to promote *Microcystis* in Gull Lake (Raikow et al. 2004, Sarnelle et al. 2005, Knoll et al. 2008, Sarnelle et al. 2010, Sarnelle et al. 2012), and that *Microcystis* can respond rapidly to large changes in mussel density (Sarnelle et al. 2012), we also anticipated that low densities of *D. polymorpha* driven by heat-induced mass mortality would have significant negative impacts on *Microcystis*. Taken together, these expectations should lead to non-monotonic responses of *Microcystis* to elevated temperatures in low-nutrient lakes invaded by *Dreissena*, which includes many hundreds of lakes in North America and Europe. We analyzed 13 years of data from Gull Lake to test these predictions.

Methods

Study site

Gull Lake is a large (822 ha), deep (33 m maximum depth, 12 m mean depth), hardwater lake located in Barry and Kalamazoo Counties in southwestern Michigan (Fig. S1). Algal production in the lake is phosphorus-limited (Moss 1972b), and summer total phosphorus concentrations in the mixed layer average ~8 μg L^{-1} (J. White, unpubl.). Details of the lake's geologic and climatic setting are summarized in Moss (1972a) and Tessier and Lauff (1992). Like other low-nutrient lakes across Michigan, *Microcystis* biomass increased markedly (from ~0% to >15% relative abundance) in Gull Lake following invasion by *D. polymorpha* in 1994 (Sarnelle et al. 2005).

Lake sampling

Weekly sampling of Gull Lake was conducted from June-August in 1998-2001 and 2005-2008, and from June-September in 2009-2014. During 2000-2001 and 2009-2011, samples were collected from a near-shore station (depth = 13 m) as well as a central station (depth = 30 m; Fig. S1). Only the near-shore station was sampled during 2005-2008, and only the central station was sampled during 1998-1999 and 2012-2014. Neither *Microcystis* biomass (paired *t*-test, $n = 28$, p

= 0.86) nor its toxin microcystin (paired *t*-test, $n = 20$, $p = 0.24$) significantly differed between sampling stations when both sites were sampled in parallel. Therefore, data were averaged across both stations for all analyses.

A vertical temperature profile from the surface to the bottom at 1 m intervals using a multiparameter sonde (Hydrolab Surveyor and Datasonde 4a) served to identify the mixed layer in the field. Lake water was collected from the mixed layer via two pooled casts of a depth-integrating tube sampler (12 m length × 2.5 cm i.d.). After thorough mixing and within 1 hour of collection, subsamples were taken for phytoplankton identification and enumeration (water preserved in 1% Lugol's iodine) and particulate microcystin (particles retained on Pall A/E glass fiber filters, 1.0 μm nominal pore size). Filters were frozen immediately for later analysis.

In the absence of quantitative biomass estimates for *D. polymorpha*, mortality rates were quantified as a function of accumulated heat exposure in Gull Lake using caged mussels as $y = 0.00029x + 0.01315$ ($R^2 = 0.67$), where x is mixed-layer degree hours >25 °C (White et al. 2015). This relationship was used to estimate temperature-dependent mortality rates of *Dreissena* for years when mortality rates were not directly measured. We also qualitatively assessed relative mussel abundance on epilimnetic sediments via visual surveys along the shoreline.

Lab analyses

Subsamples of preserved phytoplankton were settled into 10 mL tubular plankton chambers (Hydro-Bios) for enumeration via the Utermöhl inverted microscope method (Lund et al. 1958, Hasle 1978). *Microcystis* biomass was quantified from measurement of two-dimensional surface areas of all colonies in the chamber using digital image analysis software (Spot Advanced) at 100×. These measurements were converted to dry biomass using a regression fit ($\log_{10}[y] = 1.05\log_{10}[x] - 1.32$; $R^2 = 0.94$) that estimates cell density from colony surface area for Gull Lake *Microcystis;* cell density was converted to biovolume and ultimately to dry biomass using measured cell dimensions, and assuming a specific gravity of 1.0 and a wet-to-dry biomass conversion factor of 0.4 (Sarnelle et al. 2012). Full phytoplankton community counts were performed on 8 dates (4 per year in 2 different years), selected to represent the typical range of total phytoplankton biomass for Gull Lake as assessed from chlorophyll-*a* (~1.5-5.5 μg L^{-1}). Phytoplankton were identified to genus, and cell counts were made as above at a variety of magnifications (100, 400, 1000×) to accurately assess densities of both large and small taxa. Approximately 50 random fields were viewed in each of two chamber regions (outer and inner, of nearly equal surface area) to account for non-random settling of cells (Sandgren and Robinson 1984). Cell volumes (exclusive of spines, horns, and sheaths) were determined from digitized measurements of geometric dimensions (Hillebrand et al. 1999, Sarnelle et al. 2005) and converted to dry biomass as above. We then performed a linear regression of log-transformed phytoplankton dry biomass on chlorophyll-*a* ($y = 0.141x + 1.801$, $n = 8$, $R^2 = 0.62$, $p = 0.021$) to estimate *Microcystis* relative abundance as a percentage of total phytoplankton biomass for all samples.

Particulate microcystin was measured by ELISA (enzyme-linked immunosorbent assay; Envirologix QuantiPlate Kit for Microcystins visualized with a LabSystems Multiskan Microplate Reader) following three pooled 45 min, 10 mL extractions of A/E filters in 75% methanol (Harada et al. 1999).

Temperature data

Since *Microcystis* growth in nutrient-limited Gull Lake is likely a function of seasonally-integrated temperature conditions, we employed a degree day approach. The minimum temperature for *Microcystis* growth is reported to be ~15 °C (Robarts and Zohary 1987), so we computed degree days >15 °C from daily mean epilimnetic water temperature data as an index of accumulated heat during the growing season.

We monitored water temperature at hourly intervals from April-August in 2010-2014 using a vertical chain of data loggers (Hobo, Onset Corp.) through the epilimnion of Gull Lake. We constructed empirical models from this continuous record to hindcast pre-2010 water temperatures from daily mean air temperature records obtained for the entire duration of study from the Long Term Ecological Research (LTER) site at the Kellogg Biological Station (KBS, http://lter.kbs.msu.edu/datatables/12, datatable KBS002-006.27), which is adjacent to Gull Lake. We first confirmed that KBS LTER air temperature is a reasonable approximation of air temperatures over Gull Lake using nearshore data recorded in 2010 and 2012 (linear regression; $y = 0.882x + 3.527$, $n = 273$, $R^2 = 0.86$, $p < 0.001$). Air temperature was then converted to water temperature via linear regression, using separate models for the spring ($y = 1.587x + 5.955$, $R^2 = 0.84$, $n = 105$, $p < 0.001$) and summer ($y = 0.870x + 6.403$, $R^2 = 0.72$, $n = 458$, $p < 0.001$) months. These models incorporate a lag time in the response of water temperature to air temperature that maximizes model fit, as assessed with the Akaike Information Criterion (AIC; *see* Supplemental Materials, Fig. S2) (White et al. 2015).

Statistical analyses

Due to the varied duration of sampling programs prior to 2009, the declining phase of the *Microcystis* population was not fully observed in every year. Therefore, mean biomass was computed from the time of first detection through the population maximum. Mean biomass was log-transformed to stabilize the variance before statistical analysis.

The effects of accumulated degree days >15 °C on inter-annual variation in mean *Microcystis* biomass and timing of peak biomass were analyzed with linear regressions. Given the anticipated consequences of the mass-mortality event of *D. polymorpha* on *Microcystis* (*see* Introduction), we performed these regressions separately for all years (n = 13) versus excluding 2011-2013 (n = 10), during which time *D. polymorpha* densities on the mixed-layer sediments of Gull Lake were near zero at the start of the *Microcystis* growing season (White et al. 2015).

In addition to the simple regression approach above, we accounted for the effects of *D. polymorpha* density on *Microcystis* by using *D. polymorpha* mortality from the previous year as a surrogate for *D. polymorpha* density at the start of the *Microcystis* growing season. This assumes that any effect of *D. polymorpha* mortality on *D. polymorpha* density does not affect *Microcystis* in the current year, but rather the following growing season. This is reasonable since we have shown that high mussel mortality in Gull Lake occurs after a prolonged period of water temperatures >25 °C (White et al. 2015). For example, the initial mass mortality event in 2010 occurred after *Microcystis* biomass had already peaked; subsequent mass mortality of new recruits in 2011 and 2012 also occurred late in the *Microcystis* growing season. Any young-of-year *D. polymorpha* recruits that survived and successfully overwintered during these years would have low *per capita* filtering rates, and thus low impact on *Microcystis'* spring recruitment to the water column, relative to larger, older mussels (Kryger and Riisgård 1988). To explore the interaction between degree days and *D. polymorpha* mortality in the previous year on *Microcystis* biomass, we also performed multiple regression after centering the predictor variables.

Results

Microcystis mean biomass, timing of peak biomass, and particulate microcystin all exhibited substantial inter-annual variation in Gull Lake over the period of observation from 1998-2014. *Microcystis* generally first appeared in the water column in June, increased to a maximum in July or August, and then declined. The timing of peak biomass varied by as much as one month over the period of observation, from 26 July to 27 August. Peak biomass ranged from 6 to 135 μg L^{-1}, corresponding to ~3% to 80%, respectively, of the total phytoplankton biomass. On average, *Microcystis* constituted ~2-25% of the total annual phytoplankton dry biomass during the summer in Gull Lake. Mean particulate (presumably cell-bound) microcystin concentrations ranged from 0.02 μg L^{-1} to 0.34 μg L^{-1}.

Using our growing-season index of epilimnetic degree days >15 °C, annual accumulated water temperatures ranged from a minimum of 785 degree days in 2009 to a maximum of 1,021 in 2012. As reported previously, mean *D. polymorpha* mortality during the series of die-offs in 2010-2012 was ~84%; mean daily mixed layer water temperatures during this time (maximum 27.7-29.7 °C) were among the top 3% for the period of record, making these temperatures statistically extreme (Fig. 1). Photographic evidence and routine inspections of littoral mussel densities conducted each year provide qualitative confirmation of the near extirpation of *D. polymorpha* from the epilimnetic sediments in 2010 and that very low densities persisted until the summer of 2013 (White et al. 2015). Prior to the initial 2010 mass-mortality event (~100%) of *D. polymorpha,* we estimate that annual temperature-dependent mortality never exceeded the 2005 rate of 59% (1997-2009 range = 1-59%, mean = 22%). Observed mortality in 2013-2014 decreased back to near background levels (mean = 35%) when temperatures were again cooler and *D. polymorpha* re-colonized the epilimnetic sediments (White et al. 2015). All other routinely monitored physical-chemical variables (e.g., pH, dissolved oxygen, conductance) in Gull Lake were within their typical ranges during the periods of high mussel mortality (White et al. 2015).

Microcystis biomass was significantly higher and peaked significantly earlier in Gull Lake during warmer years, but only for the 10 years when zebra mussels were abundant on epilimnetic sediments (linear regressions, $n = 10$, $R^2 \geq 0.47$, $p \leq 0.028$; Fig. 2). Including years in which zebra mussels were scarce in the littoral zone (2011-2013), as a result of high mortality the year before coupled with failed recruitment, resulted in a negation of the positive effect of accumulated temperature >15 °C on *Microcystis* biomass (linear regression; $n = 13$, $R^2 = 0.11$, $p = 0.27$; Fig. 2a). *Microcystis* biomass and microcystin were reduced on average by ~74% and 81% respectively during 2011-2013, as compared to years when zebra mussels were abundant on epilimnetic sediments throughout the entire growing season (Fig. 3).

To examine the influence of mussel mortality (a surrogate for mussel density during the following growing season) on the temperature-*Microcystis* relationship across all 13 years of observation, we regressed residuals from this relationship on *D. polymorpha* mortality during the previous year. In this analysis, the influence of mussel mortality on *Microcystis* was highly significant (linear regression; $n = 13$, $R^2 = 0.57$, $p = 0.003$, Fig. 4). Greater than 60% of the inter-annual variation in mean *Microcystis* biomass in Gull Lake could be explained by the combined effects of degree days >15 °C and mortality of *D. polymorpha* from the previous year (multiple regression, $n = 13$, $R^2 = 0.62$, $p = 0.05$). As revealed by the signs of the regression slopes, degree days had a significant positive influence on *Microcystis* biomass (slope = 0.002, $p = 0.05$) while heat-induced *D. polymorpha* mortality had a significant negative influence (slope = -0.80, $p = 0.004$). This model predicts the highest mean *Microcystis* biomass (>10 μg L^{-1}) in Gull Lake when the growing season exceeds ~850 degree days >15 °C and *D. polymorpha* mortality during the previous year was below ~0.4. We did not detect a significant degree day × mortality interaction and, therefore, these reported model results do not include the interaction term.

Discussion

Disruptions to species interactions caused by climatic change and variability may have impacts that are as strong as or stronger than the direct climatic effects on any individual species, and these may operate antagonistically to one another. In stark contrast to existing climate change projections that predict increases in harmful cyanobacteria as a result of positive temperature effects on growth physiology and water column stratification (Paerl and Huisman 2008, Paul 2008, Carey et al. 2012), we observed a large decrease in *Microcystis* in low-nutrient Gull Lake during the warmest period of our 13-year study. *Microcystis* biomass increased with accumulated heat in Gull Lake only when zebra mussels were present (Fig. 2a), confirming *D. polymorpha* to be a strong facilitator of *Microcystis* in low-nutrient lakes (10-25 μg L^{-1} total phosphorus) (Raikow et al. 2004, Knoll et al. 2008). For three consecutive summers (2010-2012), sustained water temperatures >25 °C repeatedly exceeded the chronic (i.e., degree-hour) lethal threshold of *D. polymorpha,* resulting in significant mortality (≥ 92%) and failed recruitment (White et al. 2015). Although these high water temperatures (Fig. 1) are within the optimal range for *Microcystis* growth and community dominance (~25-32 °C) (Zehnder and Gorham 1960, Robarts and Zohary 1987, Imai et al. 2009), *Microcystis* dynamics during this period resembled those from the coolest years of observation, with biomass in 2012 nearly an order of magnitude lower than predicted by temperature alone (Fig. 2a).

Climate change may result in complex, non-monotonic responses of *Microcystis* to elevated temperatures in low-nutrient lakes by disrupting the critical interaction with its facilitator species. Our results could not have been predicted from existing data on the short-term responses of these two interacting species to increased temperature. Therefore, understanding how a species responds in isolation to climatic drivers, particularly in an experimental setting, does not necessarily predict the response of ecological communities in nature (Suttle et al. 2007, Post and Pedersen 2008), underscoring the need to consider species interactions in studies of ecological responses to climate change (Tylianakis et al. 2008, Van der Putten et al. 2010). Further, short-term observations of temperature tolerance may significantly overestimate temperature thresholds for mass mortality in nature. In Gull Lake, prolonged exposure to temperatures above 25 °C resulted in mass mortality of *Dreissena in situ*, whereas short-term experiments in the laboratory have identified ~30 °C to be the lethal limit for this species (White et al. 2015). Factors such as food quantity and quality may also interact with prolonged temperature stress in nature, particularly if low-quality *Microcystis* dominates the mid-summer phytoplankton community in what is already a low productivity system (Stoeckmann and Garton 2001, Vanderploeg et al. 2009).

The primary driver of *Microcystis* abundance in low-nutrient Gull Lake is unequivocally *D. polymorpha;* temperature, then, only modulates the actual biomass achieved in any given year, since the promotion of *Microcystis* by *D. polymorpha* in low-nutrient lakes is reversible upon elimination of *Dreissena*, as shown in this study, in enclosure experiments (Sarnelle et al. 2005, Sarnelle et al. 2012) and in lake surveys (Raikow et al. 2004, Knoll et al. 2008). In fact, the magnitudes of the responses of *Microcystis* and microcystin toxin (3.8× and 5.2×, respectively; Fig. 3) to the heat-induced mortality of *D. polymorpha* are highly congruent with comparative data from *Dreissena*-invaded and non-invaded low-nutrient lakes (3.6× and 3.3-8.0×, respectively) (Knoll et al. 2008, Sarnelle et al. 2010). Thus, projected distributions and abundances of individual species under future climate change scenarios that are based solely on their thermal niches may be critically misleading (Davis et al. 1998).

Our study not only illustrates some of the potential challenges for predicting a focal species' response to a changing climate, but also the need to consider how climate-induced disruptions to the spatio-temporal structure of species interactions differentially affect the participating species. For example, the mass mortality of *D. polymorpha* by August of 2010 had no discernable impact on the dynamics of *Microcystis* in 2010, as its biomass had already peaked and the population exhibited dynamics expected for a warm year in the presence of *Dreissena;* the impact of the mussel die-off on *Microcystis* was not observed until the following growing season. Likewise, although temperatures were more favorable for mussel recruitment and growth by the spring of 2013, the *D. polymorpha* population at the time *Microcystis* would have been recruiting to the water column was still characterized by a low density of young individuals with limited *per capita* filtering impact. Furthermore, *Microcystis* decreased markedly in Gull Lake despite the fact that *D. polymorpha* persisted at cooler depths below the thermocline, isolated from the mixed layer, throughout the entire period of high mussel mortality on the epilimnetic sediments (White et al. 2015). This observation implies that direct spatial overlap is a prerequisite for *Dreissena* to facilitate *Microcystis,* consistent with established feeding-based mechanisms underlying this species interaction in low-nutrient lakes. Filter-feeding *Dreissena* are known to inflict differential mortality on phytoplankton through selective rejection of collected *Microcystis* in pseudofeces*,* which may also translocate nutrients from competing phytoplankton taxa that are consumed to still-viable *Microcystis* (Vanderploeg et al. 2001, Vanderploeg et al. 2017).

Climate-induced disruptions to species interactions can occur abruptly and stochastically when driven by climatic extremes, as we observed with *Dreissena* and *Microcystis* in Gull Lake. To date, however, research on the effect of climate change on species interactions has emphasized the relatively more gradual development over time (years to decades) of spatial and temporal mismatches in the phenologies of critical life history events (e.g., migration, germination, emergence), especially in predator-prey and mutualistic relationships (Edwards and Richardson 2004, Winder and Schindler 2004, Both et al. 2006, Schweiger et al. 2008, Yang and Rudolf 2010). Yet, relatively short-duration (days to weeks), extreme climatic events such as drought and intense rainfall have been experimentally shown to affect flowering plant phenology as strongly as a decade of actual, gradual warming (Jentsch et al. 2009), and can abruptly shift the outcome of interspecific interactions between facilitation and competition in artificial plant communities (Grant et al. 2014). The importance of episodic climate events have so far received comparably less attention, and their ecological and evolutionary implications remain a research imperative (Jentsch et al. 2007).

To our knowledge, the present study is the first documented case of episodic elevated temperatures completely disrupting a species interaction in a natural community. The complete disruption of this species interaction may be a function of the high specificity of the relatively simple, two-species *Dreissena-Microcystis* system. Conversely, in a subtropical frugivore-plant mutualism, anomalous snowfall and extreme cold temperatures induced dietary shifts and extirpations among the six principal mammalian seed dispersers, greatly diminishing their collective dispersal capacity; however, the mutualistic relationship did not completely dissolve during the event, possibly due to the functional redundancy of the multi-species interaction and differential responses of the participating species, including compensatory dynamics (Zhou et al. 2013). Therefore, simpler ecological networks with limited functional redundancy might be more sensitive to climatic disruptions.

In addition to disrupting species interactions (this study), extreme climatic events can inflict high mortality within individual populations (Garrabou et al. 2009, Smale and Wernberg 2013, White et al. 2015) and thus alter population dynamics and community composition (Schoener and Spiller 2006, Thibault and Brown 2008, Wernberg et al. 2013, Woodward et al. 2015), influence primary productivity (Hoover et al. 2014), and render ecosystems more vulnerable to invasion by exotic species (Jiménez et al. 2011, Diez et al. 2012); depending on the resilience of the system, these impacts have been observed to last for months to a decade or more. Taken together, the evidence suggests that extreme climatic events can significantly affect ecosystem structure and function. Increasing climatic variability and the frequency of extreme events (IPCC 2014) may bring more rapid and potentially catastrophic disruptions within ecological networks (Scheffer et al. 2001). Due to the combined inherent statistical stochasticity of anomalous climatic events and the complexity of ecological networks, these disruptions and their impacts are challenging to understand from short-term studies; consequently, sustained, long-term monitoring of communities with respect to climatic change and variability seems essential for predicting the community- and ecosystem-level consequences of climate change.

Acknowledgments

We thank J. Berry, J. Chiotti, A. DePalma-Dow, L. Dillon, E. Fergus, S. Flemming, T. Geelhoed, B. Hanna, D. Hopper, G. Horst, M. Iadonisi, C. Kissman, C. Kozel, K. Lincoln, E.

Milroy, J. Northrop, D. Raikow, N. Sarnelle, T. Sarnelle, A. Schuerer, M. Schuetz, T. Toda, A. Wilson, D. Weed, and J. White for assistance in the field and lab. S. Bassett, T. Brownell, N. Consolatti, A. Fogiel, E. Litchman, and M. Williams provided tremendous logistical support. G. Mittelbach and P. Soranno provided feedback on an earlier version of the manuscript. We also appreciate the comments and suggestions provided by two anonymous reviewers, which improved the manuscript. This research was funded by the Environmental Protection Agency (Ecology and Oceanography of Harmful Algal Blooms/2004-Science to Achieve Results-C1, project RD83170801), the National Science Foundation (Division of Environmental Biology-0841864, Division of Environmental Biology-0841944), Michigan State University (Summer Fellowship to J. White), and the Gull Lake Quality Organization.

Figure Legends

Figure 1. Distribution of daily mean epilimnetic water temperatures in Gull Lake, June-August, 1998-2014 (*n* = 1562), including directly observed and estimated data (*see* text).

Figure 2. Gull Lake *Microcystis* abundance and timing as a function of inter-annual variation in epilimnetic degree days >15 °C: (A) mean *Microcystis* dry biomass, and (B) day of year of peak *Microcystis* biomass. Note the log scale in (A). Years with abundant zebra mussels (*Dreissena polymorpha*) on epilimnetic sediments (circles, *n* = 10) are differentiated from years (2011-2013; *n* = 3, squares) during which they were largely absent as a result of heat-induced mass mortality (*see* text). Results from linear regression analyses are for years with *D. polymorpha* only (*see* text for explanation).

Figure 3. Seasonally-averaged *Microcystis* biomass (A) and particulate (cell-bound) microcystin concentration (B) in Gull Lake in the presence (*n* = 10, black columns) versus absence (2011-2013; *n* = 3, open columns) of zebra mussels (*Dreissena polymorpha*) on the epilimnetic sediments. *D. polymorpha* was largely absent from epilimnetic sediments for most or all of the growing seasons during 2011-2013 as a result of heat-induced mass mortality (*see* text). Error bars represent ± SE.

Figure 4. Influence of *Dreissena polymorpha* fractional mortality during the previous growing season (a surrogate for *D. polymorpha* density at the onset of the current *Microcystis* growing season, *see* text) on residual variation from the temperature-*Microcystis* biomass relationship in Gull Lake. Residuals are from the linear regression of log mean *Microcystis* biomass on degree days >15 °C for all years in Fig. 2A (*n* = 13).

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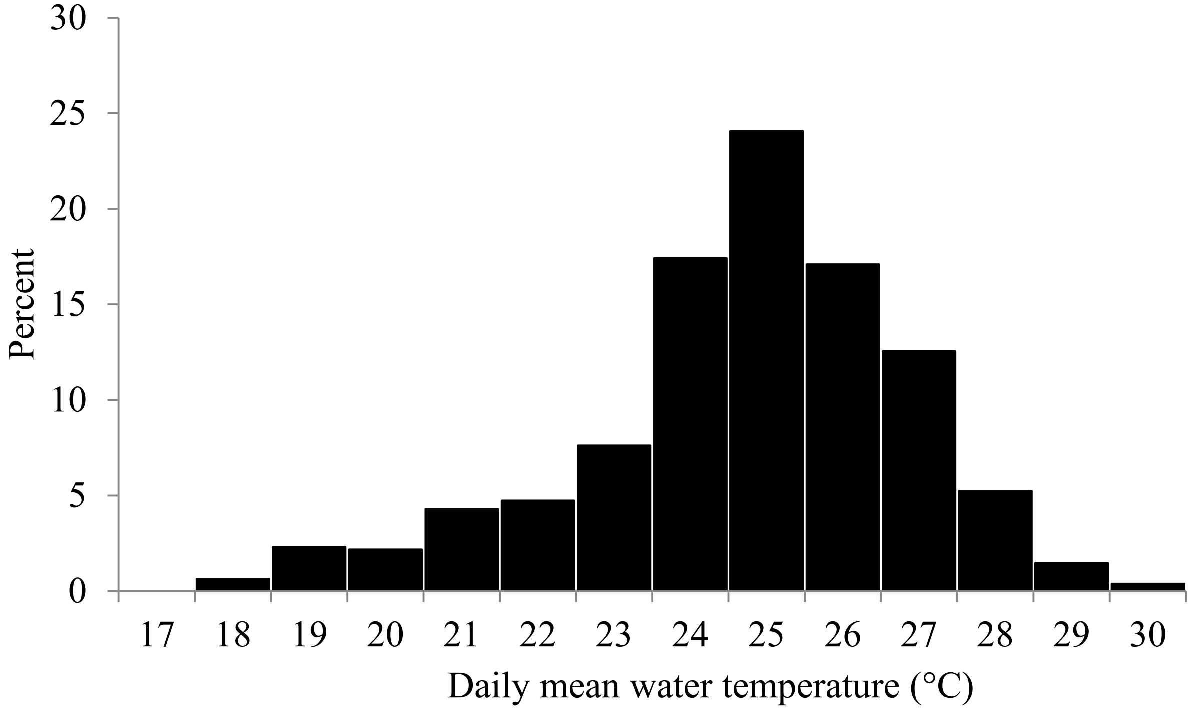
30
25
20
15
10
5
0
Percent
17
18
19
20
21
22
23
24
25
26
27
28
29
30
Daily mean water temperature (°C)

Fig. 1

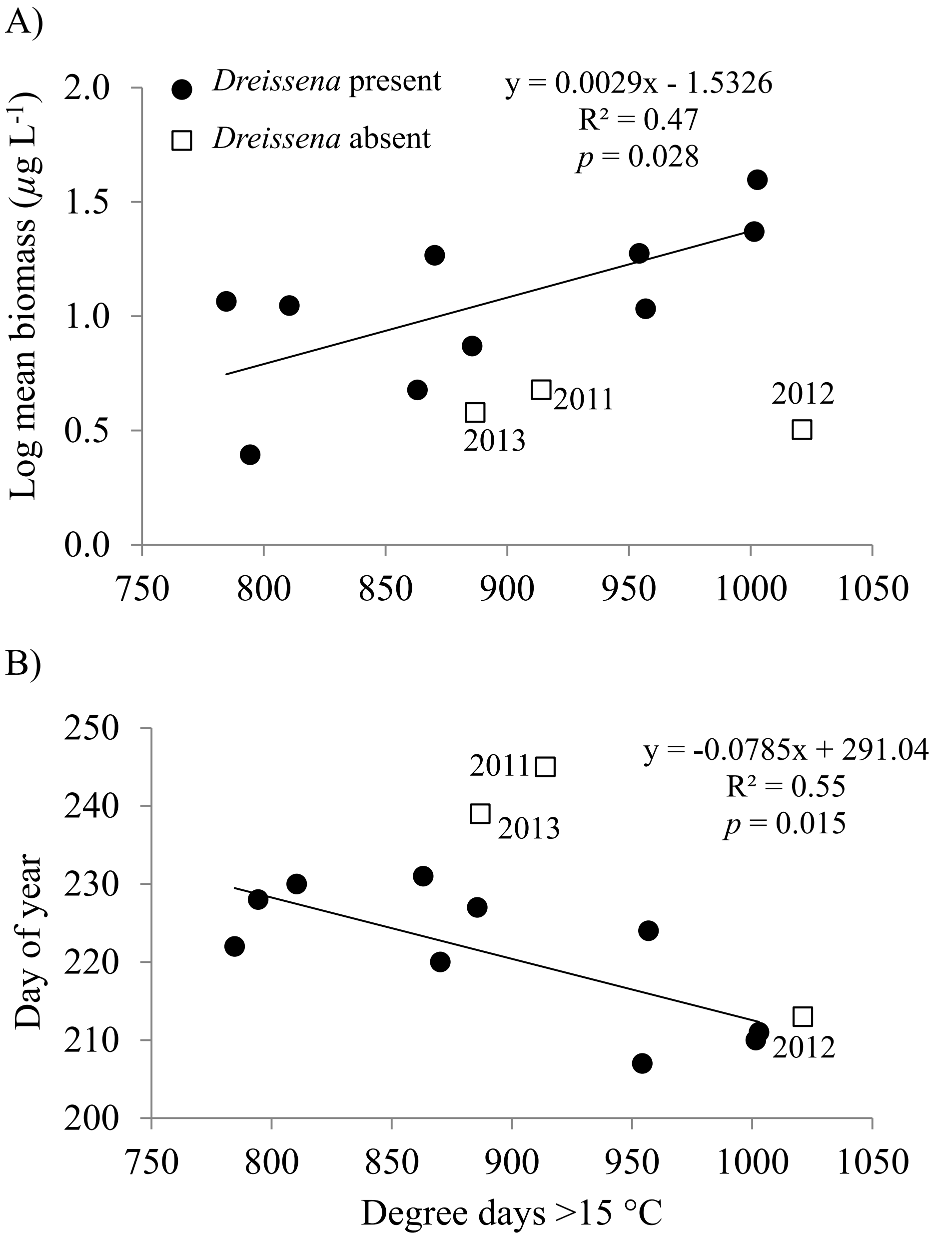
A)
Dreissena present
Dreissena absent
y = 0.0029x - 1.5326
R² = 0.47
p = 0.028
Log mean biomass (μg L-1)
2.0
1.5
1.0
0.5
0.0
2011
2012
2013
750
800
850
900
950
1000
1050
B)
250
240
230
220
210
200
Day of year
2011
2013
2012
y = -0.0785x + 291.04
R² = 0.55
p = 0.015
750
800
850
900
950
1000
1050
Degree days >15 °C

Fig. 2

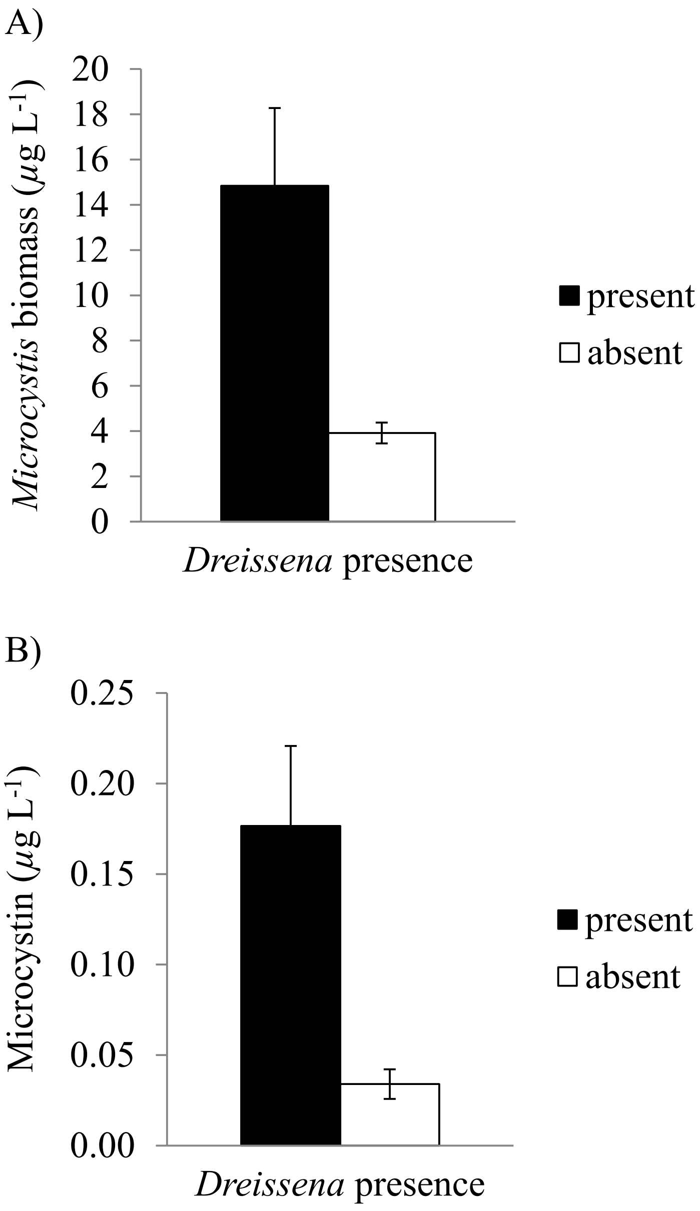
A)
Microcystis biomass (μg L^{-1})
0
2
4
6
8
10
12
14
16
18
20
Dreissena presence
■ present
□ absent
B)
Microcystin (μg L^{-1})
0.00
0.05
0.10
0.15
0.20
0.25
Dreissena presence
■ present
□ absent

Fig. 3

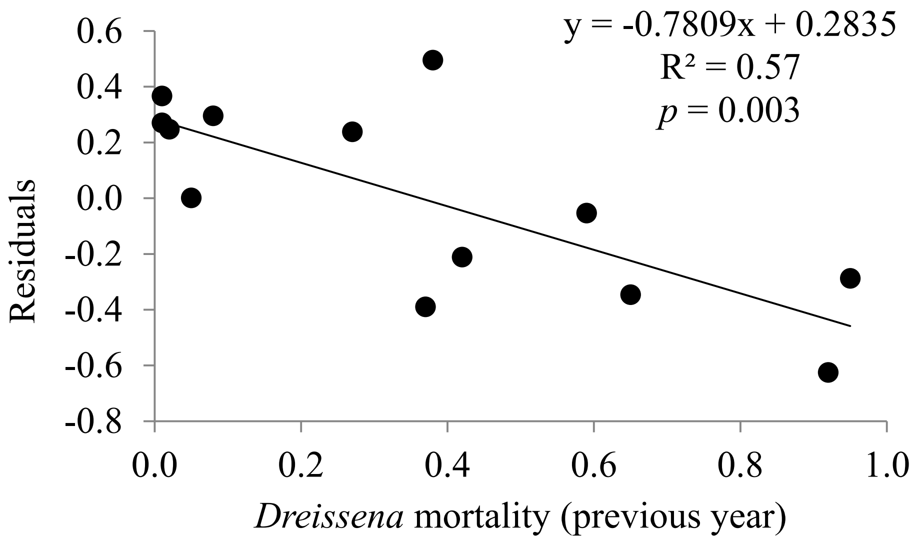
y = -0.7809x + 0.2835
R² = 0.57
p = 0.003
Residuals
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
0.0
0.2
0.4
0.6
0.8
1.0
Dreissena mortality (previous year)

Fig. 4

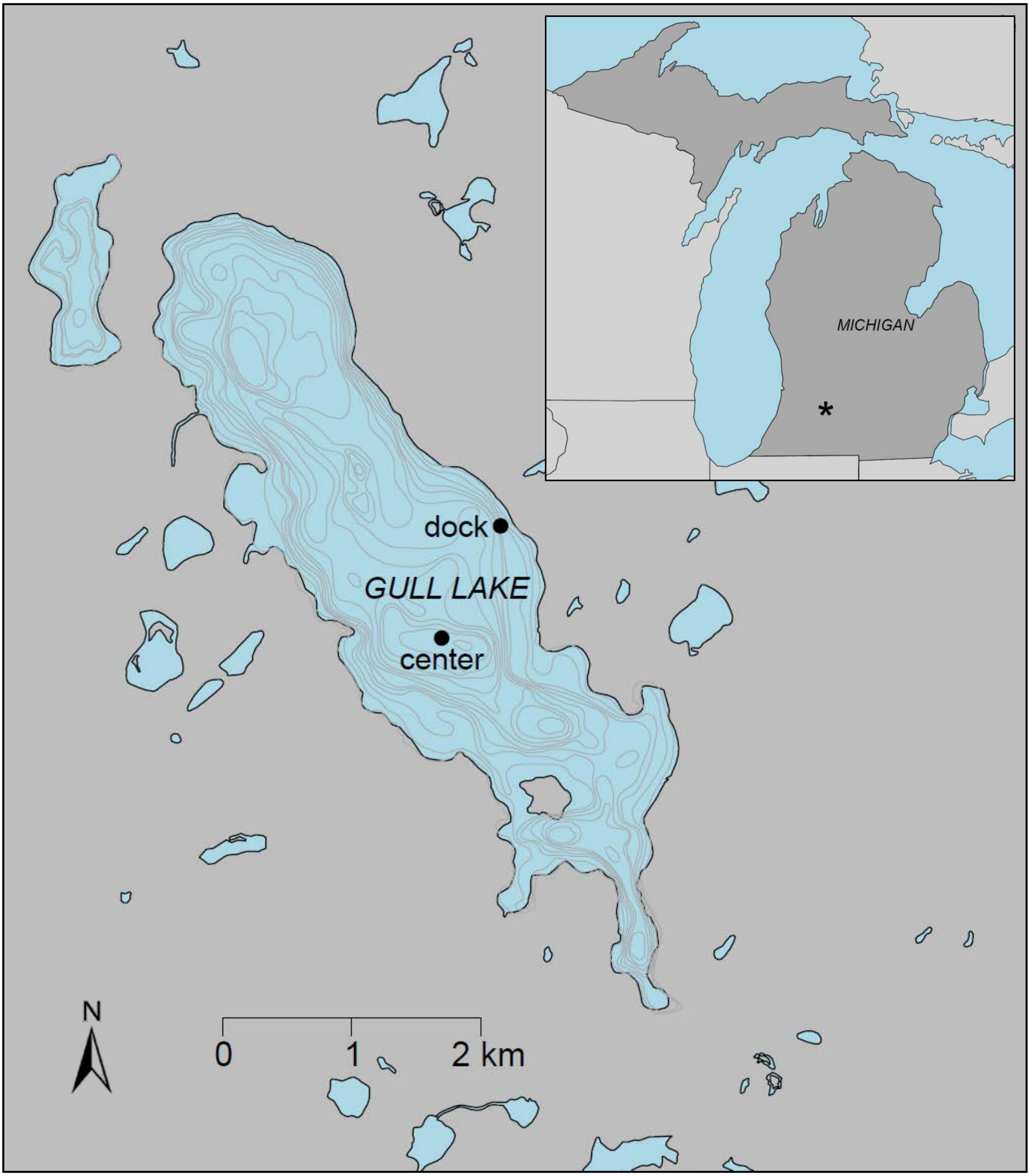

Fig. S1

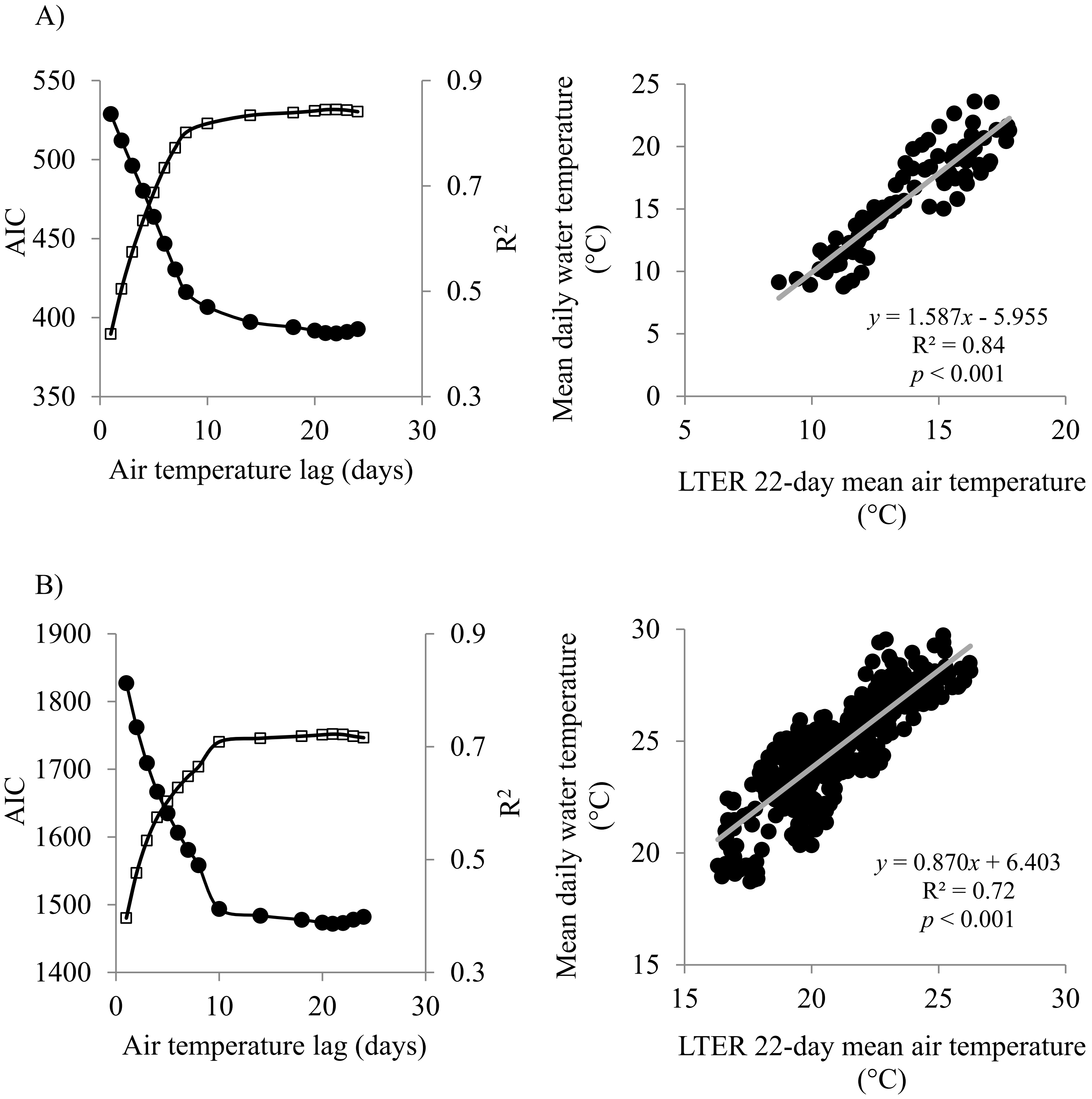
A)
550
500
450
400
350
AIC
0.9
0.7
0.5
0.3
R²
0
10
20
30
Air temperature lag (days)
Mean daily water temperature (°C)
25
20
15
10
5
0
y = 1.587x - 5.955
R² = 0.84
p < 0.001
5
10
15
20
LTER 22-day mean air temperature (°C)
B)
1900
1800
1700
1600
1500
1400
AIC
0.9
0.7
0.5
0.3
R²
0
10
20
30
Air temperature lag (days)
Mean daily water temperature (°C)
30
25
20
15
y = 0.870x + 6.403
R² = 0.72
p < 0.001
15
20
25
30
LTER 22-day mean air temperature (°C)

Fig. S2