

ARTICLE

Macrosystems Ecology

Interactions between temperature and predation impact insect emergence in alpine lakes

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Funding information

National Science Foundation; University of California Natural Reserve System; University of California, Santa Barbara

Handling Editor: Manuel T. Lerda

Abstract

While insect populations are simultaneously threatened by many local- and global-scale stressors, the interacting effects of these factors remain poorly understood. These interactions between stressors, whether additive or antagonistic, may have profound effects on our assumptions about and predictions for any given system. Here we address this gap by exploring the interactive effects of introduced predators and elevated temperatures on emerging aquatic insects across alpine lakes. Using a crossed factorial field survey, we examine whether warmer temperatures either directly affect the magnitude or diversity of insect emergence, or mediate the impacts of predation via interactions with predator presence. Based on data from more than 11,000 insects collected across a two-year period, we find a 71% reduction in insect emergence associated with an additional 3.6°C of water temperature in oligotrophic alpine lakes. While our work confirms prior findings that predator presence drives strong reductions in insect emergence, we find that the effects of predation are significantly weaker in warmer lakes (2% reduction in warmest lakes studied vs. 75% reduction in coldest). Combining our results with regional studies of predator communities to identify mechanisms suggests that the interaction effects between temperature and predator presence are likely due to changes in predator behavior across temperatures. Critically, to fully understand the multiple stressors that impact insect populations and predict their future effects, we must consider the interactions between stressors across spatial scales.

KEYWORDS

alpine lakes, benthic macroinvertebrates, emerging insects, global change, interaction effects, predator introduction, subsidies, trout

INTRODUCTION

Insects make up as much as 30% of terrestrial animal biomass (Bar-On et al., 2018) and play critical roles in

many ecosystem functions. One group of particular ecological importance and concern is emerging aquatic insects: taxa with aquatic nymph and terrestrial adult life stages. These insects feed primarily in aquatic systems

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before emerging as flying adults that cross habitat boundaries, providing nutrition to terrestrial consumers. In the process, they deliver an important subsidy from freshwaters to nearshore environments (Hoekman et al., 2011; Polis et al., 1997). As a crucial vector of habitat connectivity, emerging insects have been shown to support increased biodiversity, abundance, and health of consumers in recipient systems (Epanchin et al., 2010; Knapp et al., 2001; Kowarik et al., 2021), as well as to increase terrestrial primary production via fertilization (Dreyer et al., 2015; Wesner et al., 2019).

Because emerging insects rely on two habitats to complete their life cycle, they are particularly vulnerable to global change via disruptions in both their producing (donor) and their recipient ecosystems (Sánchez-Bayo & Wyckhuys, 2019). Such disruptions can be regional in scale, like rising temperatures (Robinet & Roques, 2010), or more localized, like predator introductions or point source pollution (Rochlin et al., 2016; Rudman et al., 2016). While these perturbations rarely occur in isolation, most ecological studies so far have focused on the responses of emerging insects to one factor at a time. Studies of zooplankton have found strong and surprising effects from interacting stressors (MacLennan et al., 2015), indicating the importance of this research. However, predicting the responses of emerging insect populations and the functions they fulfill to multiple interacting factors remains an outstanding problem. To address this gap, we considered the independent and joint effects of a local factor (trout introduction) and a regional-scale factor (increased temperatures) on the abundance, biomass, and composition of emerging insect communities. We conducted this work in the Sierra Nevada of California, USA, an alpine environment where the ecological importance of emerging insects for habitat connectivity is well established and where both local- and regional-scale environmental disruptions are prominent features.

Alpine lakes and their associated biotic communities have been considered “sentinels” of global change (Moser et al., 2019). Despite the remote and physically protected nature of many alpine lakes, these systems are relatively vulnerable to environmental factors due to their steep and sparsely vegetated catchments, dynamic weather, and intense flushing rates (Loria et al., 2020). High-elevation lakes are among the fastest warming freshwater systems worldwide (Kraemer et al., 2017) and are important refugia for endemic species and hot spots of biogeochemical cycling. While individual alpine lakes are often small, together they form an important portion of global freshwater systems: about 10% of lake area on Earth lies 2000 m or more above sea level (asl) (Verpoorter et al., 2014). In the Sierra Nevada, there are thousands of oligotrophic alpine

lakes along several gradients of size, elevation, and connectivity, all of which share an underlying climate and geology. In addition, many biotic populations have been well surveyed in Sierra lakes, providing regional context for trophic interactions (Knapp et al., 2020). Thus, further sampling in the context of this well-studied system can produce results with relevance to important alpine systems in other regions.

As a local threat in Sierra lakes, we focused on predator introductions because of their strong impacts and global prevalence. Salmonidae (salmon and trout) are a predator taxon commonly introduced into lake systems, due partly to their high value for fishing and aquaculture. The introduction of salmonid taxa is associated with a wide range of ecosystem effects in many lake regions (Cucherousset & Olden, 2011). Predator introductions disrupt the emergence of insects from both lake and stream systems, with cascading consequences up and down food chains (Baxter et al., 2004; Nakano & Murakami, 2001). In the Sierra Nevada of California, lakes stocked with introduced trout have fewer benthic insect larvae compared with fishless lakes (Knapp et al., 2005), with reductions disproportionately among the larger taxa (Knapp, 1996). At stocked lakes, compared with fishless lakes, fewer birds nest around the shoreline due to lower mayfly emergence (Epanchin et al., 2010) and insectivorous bats exert higher foraging effort, possibly indicating lower quality prey (Gruenstein et al., 2021). Introduced fish drive out endemic taxa, which ordinarily would rely on the same prey as the trout, such as the mountain yellow-legged frog in the Sierra (Knapp & Matthews, 2000), and displace the native fish that feed terrestrial bear, otter, and osprey populations in Yellowstone National Park (Koel et al., 2019).

As a broader scale threat to lake ecosystems, we focused on changing water temperatures, since temperature is driven by regional climate and affects many aspects of aquatic systems. Recent reviews have shown that in mountain lakes, hydrological regime (Medina & Westbrook, 2021), zooplankton production and diversity (Caldwell et al., 2020), and phytoplankton abundance (Loria et al., 2020) can all respond to shifts in temperature. However, in contrast to established effects of predators on insect emergence, the effects of changing lake temperature on emergence are complex and generally less well understood. Higher mean water temperatures may directly alter insect community composition and abundance through effects on habitat suitability or consumer–resource interactions (Toro et al., 2020), enhance or depress their food sources by changing within-lake processing of nutrients and organic matter (Bergström et al., 2013; Greig et al., 2012; Hoekman et al., 2011), or shift the timing of emergence differentially across taxa (Belitz et al., 2021; O’Gorman, 2016). Insects experiencing warmer temperatures

may develop faster with smaller bodies (Dickson & Walker, 2015; Li et al., 2011; Maier et al., 1990) or grow to a larger adult size than low-temperature controls (Gregory et al., 2000; Nelson et al., 2020).

Importantly, we also focused on the interaction between these two stressors. A meta-analysis of field data from lakes in the Canadian Rockies and Klamath Range showed that insect emergence was lowest and predator introduction was least impactful at warm (low elevation) sites (Piovia-Scott et al., 2016), while controlled mesocosm studies in tanks modeled on alpine ponds led to an apparently opposite conclusion that warming both increases insect emergence and magnifies the effect of predatory fish (Greig et al., 2012). The contradiction between these findings is a reminder that context-dependent interaction effects often cause systems to respond in unexpected ways (Jackson et al., 2016). Mesocosm studies, while often critical to determine mechanistic effects of one or two factors, may not be directly comparable with real systems. Given the multiple and overlaid nature of disruptions from global change, it is critical to understand how these threats will interact to shape ecological systems in the future.

To better understand the interactions between co-occurring perturbations, this study leveraged a natural experiment of predator introduction and removal across temperature gradients to identify and separate the effects of water temperature and predator presence on insect emergence from lakes. Specifically, we took advantage of the varied nature and high number of Sierran lakes to establish a crossed factorial field survey to determine whether increased temperatures can either directly affect the magnitude or diversity of insect emergence from lentic systems, or mediate the impacts of predation via an interactive effect with trout presence. We addressed these questions by measuring the abundance, biomass, average body size, and diversity of emerging insects over the course of two summers from six lakes in Humphreys Basin in the south-central Sierra Nevada, selected for their overall similarity except in temperature and predator presence.

We predicted that the abundance and biomass of emerging insects would be (1) negatively associated with predator presence, (2) positively associated with warmer temperatures, and (3) less impacted by predator presence in warmer lakes, following the results of Piovia-Scott et al. (2016). We also compared insect community composition across lakes, expecting that compositional shifts might help explain any observed changes in insect biomass. We predicted that warmer lakes would support a higher abundance and diversity of insects (following Greig et al., 2012) and of other invertebrates (surveyed in the Sierra Lakes Inventory Project; Knapp et al., 2020), potentially leading to predator satiation or preventing

the introduced predators from effectively capturing all the insect larvae. Results from this work provide specific insight into some of the mechanistic drivers of insect emergence and how increased water temperatures, changes in predator assemblage, or their interaction should be expected to affect emerging insects and the subsidies they provide. More broadly, these results highlight the critical interactions between regional and local stressors in predicting the magnitude and even direction of impacts from a particular factor on at-risk insect populations and the services they provide.

METHODS

Study sites

The Sierra Nevada of California is a mountain range located near the western coast of North America, containing more than 4000 high-elevation lakes which provide an ideal laboratory to examine the interacting effects of multiple global changes. Much of the mountain range is protected as wilderness, preventing many direct impacts of anthropogenic development, but the system is still vulnerable to both local and regional stressors. Sierran lakes at high elevation lack endemic fish populations due to physical barriers to dispersal. Many of the lakes have been stocked over the past hundred years with trout species (*Oncorhynchus mykiss* and *Salvelina fontinalis*) to improve recreational fishing opportunities. In addition, temperature in these lakes is largely regulated by snowpack and duration of winter ice cover (Sadro et al., 2018), and therefore varies with elevation and catchment characteristics as well as interannually.

We surveyed six oligotrophic lakes in the Sierra, three with and three without fish populations, across an elevation range between 3400 and 3650 masl that represent a gradient of temperature (Figure 1D). These lakes are within the same catchment (Humphreys Basin, California, USA, Sierra National Forest; 37.26° N, 118.70° W) to facilitate comparison, and have been considered as pairs in previous studies on fish effects due to similarities in depth, substrata, and catchment features (Epanchin et al., 2010; Pope et al., 2009). We conducted surveys of lake substrata and sampled water quality to confirm similarity (Appendices S3 and S4). All lakes were oligotrophic and dilute, with predominantly rocky catchments and littoral zones and little to no emergent vegetation. Principal components analysis (PCA) confirmed that the presence of fish and the temperature gradient were not confounded with other abiotic factors such as lake depth, size, or catchment area. Lakes with fish had previously been stocked with *S. fontinalis* (the coldest lake) or *O. mykiss*

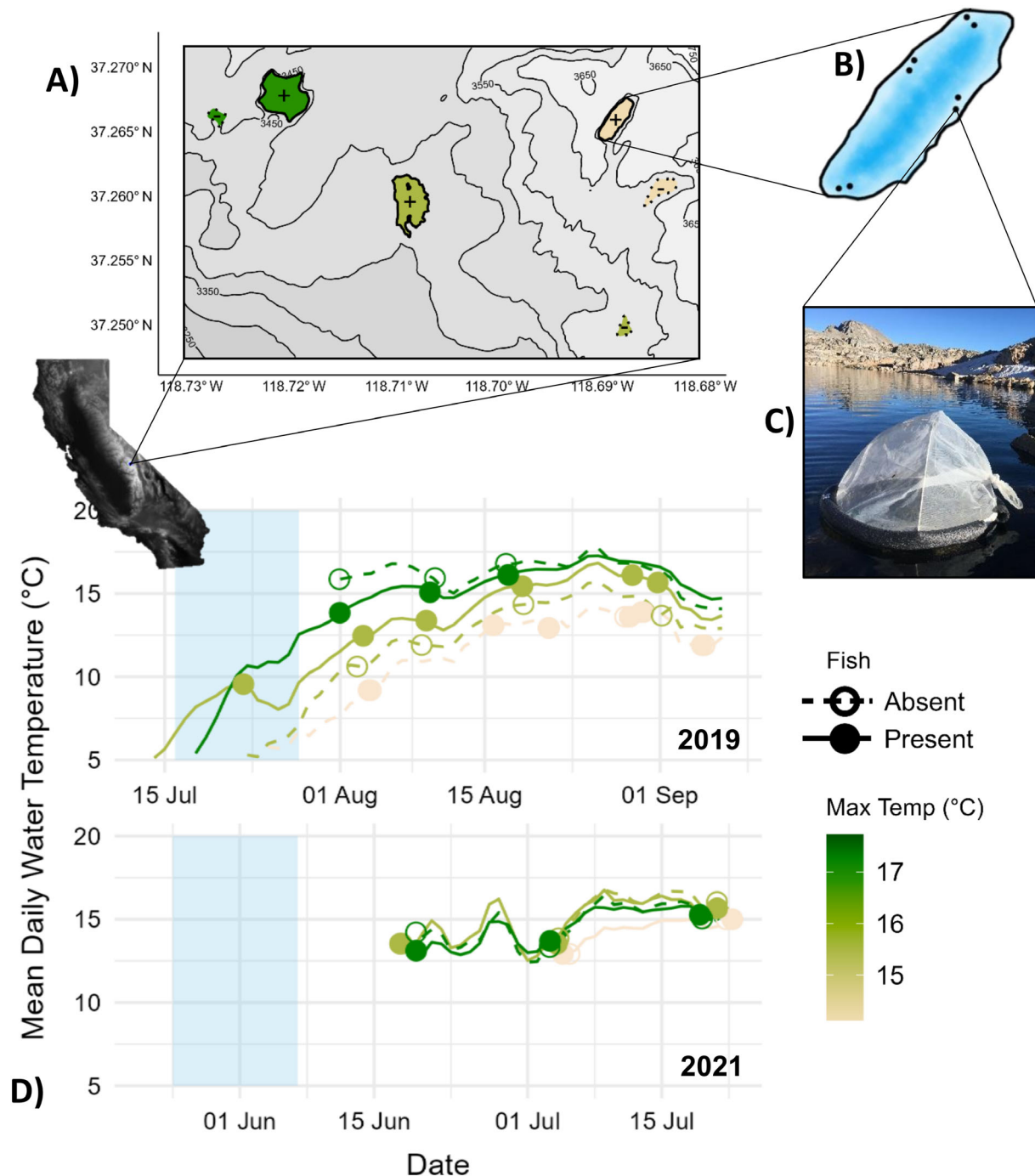


FIGURE 1 Location, timing, and methods of emergent insect sampling. (A) Location, fish status, and relative water temperature of six study lakes along an elevation gradient in the central Sierra Nevada. Lake names are provided in Appendix S1: Table S1. (B) Bathymetric map of one study lake (cold, with fish) and approximate distribution of emergence traps in the littoral zone. (C) Image of the floating traps (area 0.27 m²) used to capture insects from the littoral zone of each lake. (D) Water temperatures recorded in the epilimnion of each lake over the course of 2019 and 2021 sampling periods (lines), along with the dates at which samples were collected from each lake (circles). Blue boxes show the approximate dates in each year when the study lakes became ice-free.

(middle and warmest lakes), both omnivorous visual predators with similar effects on insect prey, and now contain sustaining populations of one or both species (Erdman, 2013) at comparable densities, with the fewest fish per hectare in the coldest lake (Armstrong & Knapp, 2004).

Abiotic parameters

To quantify lake temperature, we deployed Onset HOB0 temperature loggers by anchoring them at approximately 0.5–1 m depth underwater near the outlet of each lake in

both 2019 and 2021 (as early as June and as late as September across the two years), where they experienced temperatures roughly equivalent to an integrated average of the lake epilimnion and recorded them at 10–15 min intervals. We used these readings to calculate mean daily temperatures for each lake, as well as to determine the peak water temperature reached by each lake in each year. We conducted sensitivity analyses that confirmed that neither the choice of temperature variables (mean vs. minimum, maximum, or range) nor any potential solar heating of the loggers affected the direction or significance of our results. In addition, we used visual inspection of daily satellite imagery (Planet Labs Team, 2017) to determine approximate dates of ice-off at each lake by finding the first day without visible ice at each lake. In cases where there was no clear imagery of a day with ice followed directly by a day without ice, we supplemented with field notes or selected the midpoint of the window between the last image with ice and the first ice-free image.

Insect trapping

During the summers of 2019 and 2021, we used floating emergence traps (Figure 1C, modified from Pope et al., 2009) to collect adult insects as they emerged from the surface of each lake. We deployed traps for 24 h to capture the full diel cycle of emergence; in addition, we anchored them over a variety of substrata (cobble, sediment, boulders, and gravel) to collect a sample of emergence from the various lake littoral habitats. A total of eight traps per lake were deployed on each sampling date, with two traps placed in 1–2 m of water at each cardinal direction of the lake during each visit. Each trap covered 0.27 m² of the lake area. Samples were collected on the same day from pairs of lakes (one with and one without fish) to control for daily variation in weather. In 2019, we visited each lake pair 3–6 times between ice-off (mid-July) to late summer (early September) in order to capture seasonal trends in emergence. In 2021, we focused our sampling closer to the seasonal peak in emergence identified during 2019; specifically, we visited each lake pair three times across early to mid-summer (mid-June–late July), with approximately 2 weeks between each visit. All sampling was conducted in fair weather (i.e., not during thunderstorms, rainstorms, or high wind events).

We aspirated all visible insects (minimum size is approximately 0.75 mm) from each trap and preserved them in 70% ethanol. All samples were then stored at –20°C to further protect against degradation prior to sorting and identification. Insects were identified to

taxonomic order using a dissecting scope (magnification 8×–63×) and dichotomous keys (Behm & Seltnann, 2019; Usinger & Bentinck, 1974). We identified Diptera to family or genus using the same methods and resources. For Dipteran taxa where finer taxonomic resolution was difficult (e.g., Chironomidae), we assigned specimens to size classes (0.75–1.5 mm, >1.5–3 mm, >3–5 mm, and >5 mm length) based on their length from head to abdomen measured via handheld micrometer or calipers. For each taxonomic group or size class, we measured the head-to-abdomen length of at least 10 individuals using a handheld micrometer and dissecting scope at a magnification of 8×–63×. We used these values to calculate biomasses following the methods of Sabo et al. (2002). We scaled all measurements of emergence to the surface area of the traps (0.27 m²) and reported results as a rate of emergence per square meter of lake per day.

Statistical analyses

Model fitting and selection

Annual peak lake water temperature was selected as the best variable to describe between-lake climate differences, as it provided the most consistent comparison across sites and years with differing lengths of temperature records (Figure 1D) and is the most directly interpretable measurement of temperature effects on insect populations; however, models run with alternative climate variables such as lake elevation, ice-off date, or duration of ice cover gave similar results. Similarly, using daily mean water temperature, daily maximum temperature, nightly mean temperature, or number of days since ice-off as an indicator for seasonality all resulted in similar conclusions, so daily mean water temperature was used for simplicity across all models. We checked for collinearity between all predictors before conducting analyses and used PCA to check for additional confounding variables (Appendix S1). Because multiple traps were deployed during each sampling date, dates were spread across two years, and insect emergence depends on weather conditions, we assumed a violation of independence between data points collected on the same date. This assumption was confirmed by clumped patterns in the residuals when a linear model was fit to the data. We therefore fit generalized linear mixed models (GLMMs) with a random effect of sampling date to our response variables of emerging insect biomass, abundance, and body size to determine which environmental variables best predicted insect emergence after taking this within-day and within-year correlation into account. Each model

included a fixed effect for climate (peak annual water temperature), seasonality (daily mean water temperature), fish status, and the interaction between fish status and peak temperature. The model structure was as follows:

$$\text{Emergence} \sim \text{fish status} \times \text{peak temperature} + \text{daily temperature} + (1|\text{sampling date}) \quad (1)$$

Insect biomass and individual body size were log or square root transformed to obtain normal residuals and modeled with a Gaussian error structure. Because abundance was a count variable with high dispersion and relatively few zeroes, we used a truncated negative binomial distribution with a constant zero-inflation term to model insect abundance. We used the R packages *glmmTMB*, *DHARMA*, and *MuMIn* to construct, evaluate, and compare models for each response (Barton, 2020; Brooks et al., 2017; Hartig, 2022) in R versions 3.6 and 4.1.2 (R Core Team, 2021). We used the *DHARMA* functions *testResiduals* and *testQuantiles* to eliminate any models that violated dispersion or homoscedasticity assumptions, and then used backward stepwise selection to find the best model for each response (lowest corrected Akaike information criterion [AIC_c]). Marginal mean effects of peak water temperature and fish presence were calculated for each model using the *emmeans* package in R (Lenth, 2022) (Figure 2).

Ordination

To determine whether emerging insect communities differed between lakes, we performed nonmetric multidimensional scaling (NMDS) using the *vegan* package in R (Oksanen et al., 2022). We pooled samples by year from each lake and plotted rarefaction curves in order to ensure that each lake-year combination had been adequately sampled (Appendix S5). We standardized the insect counts across taxa from each pooled community using Wisconsin and square root transformations to reduce the influence of outlying taxa. We then calculated the Bray–Curtis distances between the 12 standardized lake communities and input the resulting distance matrix into the *metaMDS* function with *autotransform* turned off to create NMDS plots. We also ran a permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function (Anderson, 2017; Oksanen et al., 2022) on the same distance matrix using fish status, peak lake temperature, and their interaction as predictors in order to determine whether any of those environmental variables

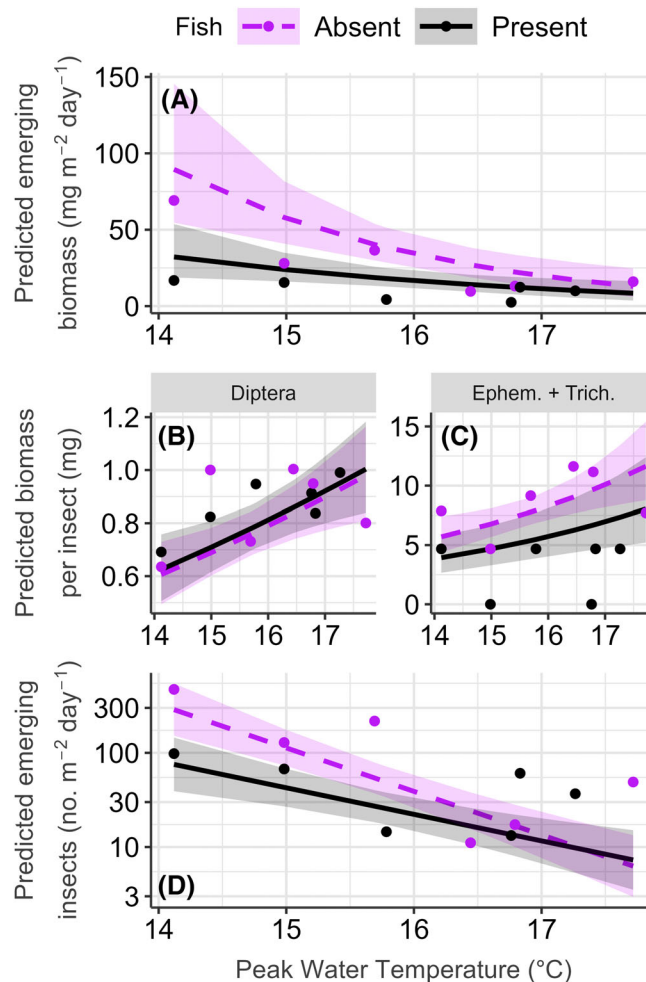


FIGURE 2 Effects plots for models based on data from individual traps ($n = 311$). Lines represent the influence of peak water temperature (x-axes), introduced predator presence (color + line type), and their interaction on various metrics of emergence from six lakes across two years. Points represent mean data values for each year and lake. (A) Temperature and predator introduction both decrease the overall biomass of subsidies from these lakes. (B, C) Temperature increases the mean body size of emerging insects, while predator introduction decreases mean body size only among Ephemeroptera (Ephem.) and Trichoptera (Trich.). (D) Temperature and predator introduction both decrease the abundance of emerging Diptera, and their interaction moderates this effect.

were significant drivers of differences in community composition.

RESULTS

Specimen collections

In total, we collected 11,427 individual insects from 335 traps (221 traps in 2019, and 110 traps in 2021) over

50 separate lake-nights (34 in 2019 and 16 in 2021, Figure 1D). Some traps failed during deployment and were therefore excluded from the analysis. The vast majority (96.6%) of insects collected from emergence traps were Diptera (flies), while 0.8% were Trichoptera (caddisflies) and Ephemeroptera (mayflies). Within Diptera, 85% of total insects collected belonged to the Chironomidae, with 40% of traps capturing only Chironomidae. Other Diptera families collected included Culicidae, Tipulidae, and Simuliidae. We omitted fully terrestrial specimens (2.6% of collections) such as Coleoptera (flower beetles and weevils), Arachnidae (spiders), and Hemiptera (true bugs, mostly leafhoppers) from our statistical analyses. Odonata (dragonflies and damselflies) were not captured and are generally absent from the Sierra above 3000 m (Piovia-Scott et al., 2016).

At each lake, emergence was low shortly after ice-off and at the end of the summer and peaked between 25 and 40 days after ice-off in both years (Appendix S1: Figure S1). The total number of insects captured in each trap varied widely, from 0 to over 1500, with a median of 7 (Figure 2D). Maximum mean daily water temperature ranged from 14.1 to 17.7°C across lakes and years (Figure 1D).

Abundance, biomass, and body size across lakes

Across all temperatures, presence of an introduced predator (trout) was associated with 65% lower rates of emerging biomass (Table 1, Figure 2A). From the coolest lakes to the warmest lakes, we observed a 71% lower daily emerging biomass of insects that coincided with the 3.6°C increase in annual peak water temperature (Table 1, Figure 2A),

contrary to our hypothesis. The interactive effect of temperature and predator presence on rates of emerging biomass approached significance ($p = 0.069$, Table 1), suggesting that predator presence mattered more for insect biomass in cold lakes.

Predator presence and peak water temperature were each also negatively associated with daily numerical abundance of emerging insects (Figure 2B). The lower abundances associated with higher temperatures were attributable to reduced numbers of emerging Diptera. There was a strong interactive effect of temperature and predator presence on the numerical abundance of emerging insects and of Diptera in particular (Figure 2D, Table 1). While predators always reduced the abundance of emerging Diptera, this effect size was larger in cold lakes than in warmer lakes (Figure 2B, Table 1). Because the largest effect size occurred in the lakes with lowest trout densities and biomass, the interaction between trout presence and temperature would likely have been even more pronounced if calculated for equivalent biomasses of fish.

Predator presence was associated with reduced body size among Ephemeroptera and Trichoptera, but had no significant effect on the mean body size of Diptera. Peak water temperature was positively associated with larger individual body size for all measured insect groups (Table 1, Figure 2B,C). There were no interactive effects of temperature and predator presence on body size for any taxa.

Species composition across lakes

NMDS analysis followed by PERMANOVA revealed that predator presence and peak water temperature, but not

TABLE 1 Coefficients (β) and their significances (p values from t tests) for the best fit models of each response, selected from appropriately specified options based on smallest corrected Akaike information criterion (AIC_c) (Equation 1).

Modeled response variable	Transf. used	Fish presence		Peak annual temperature (°C)		ΔAIC_c	Fish:temp interaction	
		β	p	β	p		β	p
Total insect biomass ($\text{mg m}^{-2} \text{ day}^{-1}$)	Log + 1	-3.45	0.0243	-0.48	<0.0001	-1.23	0.18	0.0690
Diptera body size ($\text{mg individual}^{-1}$)	Square root	0.012 ^a	0.552 ^a	0.059	0.00205	+2.09
EPT body size ($\text{mg individual}^{-1}$)	Square root	-0.37	0.000893	0.20	0.00159	+2.21
Total insect abundance ($\text{no. m}^{-2} \text{ day}^{-1}$)	N/A	-7.18	0.000781	-1.06	<0.0001	-6.04	0.41	0.00248
Diptera abundance ($\text{no. m}^{-2} \text{ day}^{-1}$)	Log + 1	-7.75	0.000414	-1.10	<0.0001	-6.64	0.45	0.00125

Note: ΔAIC_c column shows the change in AIC_c that resulted from adding the interaction between fish status and peak annual temperature to the model. Each response was transformed to obtain normal residuals and was predicted using a generalized linear mixed model with Gaussian error structure, except for abundance (counts), which were not transformed and were fit with zero-inflated truncated negative binomial family structure to account for zero-deflation and overdispersion. "Transf. used" column indicates which transformation was used for each response. All models included a random effect of sampling date within sampling year (Equation 1). EPT stands for Ephemeroptera, Plecoptera, and Trichoptera (large-bodied, sensitive invertebrate taxa).

^aFish was not a significant predictor of Diptera body size, but had to be kept in the model to obtain appropriately distributed residuals.

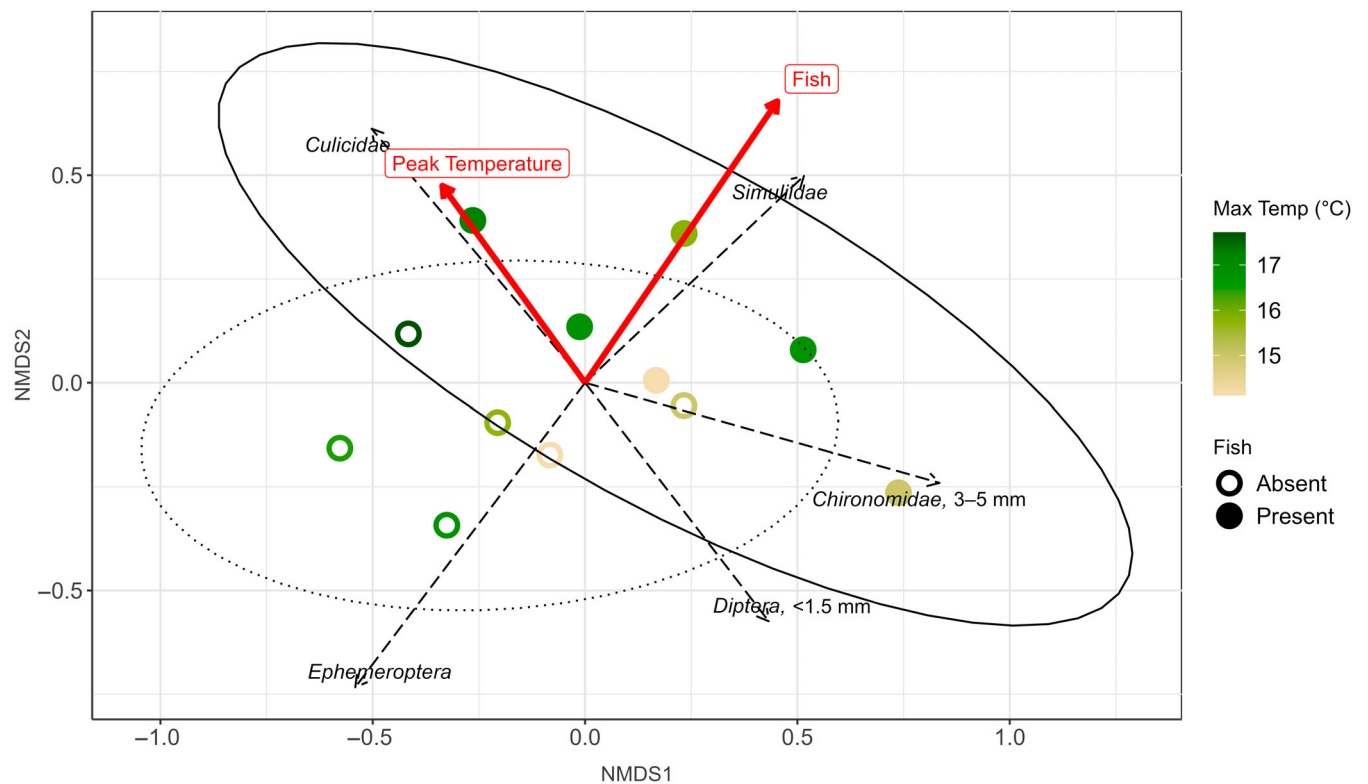


FIGURE 3 Nonmetric multidimensional scaling (NMDS) plot showing the community composition of insects emerging from each lake in 2019 and 2021. NMDS stress = 0.088 over two axes. Ellipses represent the 95% CI for sites with fish (solid line) and without fish (dotted line). Taxa labeled in plot were all significant drivers of community variation at a significance level of 0.05. NMDS was performed on a Bray–Curtis distance matrix of standardized community counts. Peak temperature and fish status were both significant drivers of differences in community composition based on a permutational multivariate analysis of variance, while year was not.

their interaction, were significant correlates of emerging insect community composition (Figure 3). NMDS with two dimensions was sufficient to represent the variation in communities (stress = 0.088). Lakes without fish tended to have fewer Simuliidae, but more Ephemeroptera. While Ephemeroptera and Trichoptera accounted only for 0.95% of individuals in traps from lakes without fish, they accounted for 52.6% of biomass in those traps due to their larger body sizes.

Warmer lakes had more Culicidae than cooler lakes. Cooler lakes had more medium-sized Chironomidae and more of the smallest size class of Diptera (≤ 1.5 mm length, various taxa). Other taxa also differed along the axis of temperature, but not significantly (Figure 3). Large Chironomidae were a small proportion of the insect community, but were more important in warmer lakes.

DISCUSSION

We found that emerging insect communities in warmer lakes had lower abundances, larger bodied Diptera, and

less responsiveness to predator presence than those in cooler lakes. This was likely due to metabolic limits on predator behavior, as trout forage less effectively in warmer waters. Additionally, data from regional surveys showed that warmer lakes had larger populations of small grazers such as rotifers and copepods (Appendix S2). These taxa could have competed with the smaller Diptera taxa and caused the observed shift in the insect community toward larger bodied individuals. While our findings contradicted some of our initial hypotheses, they link together results from previous studies and provide insight into the potential responses of oligotrophic lakes to global change.

The presence of introduced predators (fish) was associated with a mean 65% reduction in emerging insect biomass across temperatures (Figure 2A). Such observed decreases align with other studies that have documented similar decreases in emergence associated with introduced trout taxa (Epanchin et al., 2010; Knapp et al., 2001; Pope et al., 2009). We additionally found that the effect of predators varied with lake temperature, with the effect of fish on the numerically dominant group, Diptera, weaker in warm lakes than in cold (Table 1).

While the brook trout species in the coldest lake may be more effective predators than the rainbow trout in the warmer lakes, the interaction term between temperature and fish presence remained important when models were fit without the coldest pair. The brook trout-containing lake also had greater overall abundances of emerging insects than the warmer rainbow trout-containing lakes, further suggesting that predation differences between trout taxa were unlikely to drive our results.

The 3.6°C gradient in peak lake temperature across this study was associated with a reduction in total emerging insect biomass of 71% at warmer temperatures (Figure 2A, Table 1). While less well studied than predation effects, the relation of temperature to emerging insect abundance has proved to be divergent with work suggesting both decreases (Hogg & Williams, 1996) and increases (Greig et al., 2012) in insect emergence from mesocosms warmed by 2–3.5°C above ambient temperatures. Although temperature effects could have been related to minor differences in the availability of shallow littoral habitat, we find this unlikely as previous work has shown that lake mean depth does not alter the impact of trout predation on chironomid taxa (Weidman et al., 2011) and our PCA found no significant association of temperature with lake depth (Appendix S1: Figure S2). Cumulatively, these results show that the temperature gradient observed in our study—well within projections for future warming of freshwater systems worldwide (O'Reilly et al., 2015)—is biologically relevant to freshwater invertebrates. Alpine lakes are therefore highly vulnerable to the effects of warming despite their remote nature and physical protection.

The reduction in emerging biomass that accompanied warmer temperatures in our study lakes was attributable to a lower abundance of emerging insects (Figure 2D), which outbalanced the simultaneous increase in mean individual body size across all measured groups (Figure 2B,C). A significant negative effect of temperature on abundance of emerging Diptera, the most numerically abundant group, supports this conclusion. This biomass reduction, likely driven by increased competition and changes in predator behavior, is consistent with patterns of biomass loss from other aquatic and marine systems (Bowler et al., 2017). For example, ensemble projections from six models predicted a 5% drop in total animal biomass in global oceans for each degree Celsius of future warming (Lotze et al., 2019). Specific to emerging insects, experimental stream and pond warming studies have found a significant reduction in the abundance of Chironomidae at 2–3.5°C above ambient temperatures (Hogg & Williams, 1996; Jonsson et al., 2015). If common emerging insect taxa are likely to decrease in abundance under moderate warming,

then many near-term global change scenarios will lead to significant reductions in emergence—even in the absence of local stressors such as predator introduction.

We also found consistent interactive effects between temperature and predator presence on total biomass, driven by Diptera abundance: predator presence had less of an effect on biomass and on Diptera abundance in warmer lakes (Table 1). This result differs from conclusions of a mesocosm study where the temperature of stocked cattle tanks was manipulated (Greig et al., 2012). In that study, both emerging insect biomass and the negative effect of predators increased with warming. The discrepancy between these findings and ours suggests that perhaps in the mesocosm study, increased individual body size with temperature was not balanced by a reduction in emerging insect abundance as it was in actual lakes. Lower abundance of insects emerging from the warmer lakes in this study must therefore have been driven by trophic- or organismal-level mechanisms that differ along a temperature gradient, not solely by the abiotic mechanisms that are the most obvious results of warming. We find the most likely explanation to be changes in predator behavior, which we explore along with alternatives below.

Behavioral and metabolic explanations

The most likely explanations for our otherwise unexpected findings are behavioral changes that separate predators spatially from their invertebrate prey. Data from Castle Lake in California, a mesotrophic alpine lake with similar fish and invertebrate communities, show that warm temperatures (above ~15°C) can prevent fish from foraging as much in the littoral benthic zone, as the warmer water there is less metabolically favorable for them (Caldwell et al., 2020). That study showed that in warmer years, fish relied more on planktonic food sources and less on benthic invertebrates—despite little or no change in the population abundances of those prey from the colder years when they were highly important to fish populations.

Such a behavioral shift among introduced trout could contribute to the findings from this study that predation exerted a greater negative impact on emerging Diptera in cooler than in warmer lakes. It may also suggest why predation effects on Trichoptera and Ephemeroptera were constant across temperatures because these larger, more rewarding prey items might have led predators to forage in the littoral zone despite the less favorable higher temperatures. Our data therefore suggest that understanding systemic responses to global change requires

considering behavioral responses as well as trophic and physical ones.

Another organismal-level explanation, metabolic requirements of predators or prey that scale differently with temperature, was less likely to explain the interaction effects we found. For ectothermic predators such as trout, warmer temperatures lead to higher baseline metabolic rates and therefore higher caloric needs (Brown et al., 2004; Durhack et al., 2021). When invertebrate metabolic rates increase under warmer conditions, the individuals may sometimes mature faster or grow larger (Gregory et al., 2000), or conversely, reach reproductive maturity at a smaller size (Larsen et al., 2016; Li et al., 2011). This increase in predator metabolic and foraging rates with warmer temperatures, not necessarily matched by an increase in available larval prey, would predict a strong interactive effect such that introduced predator effects were more important in warmer lakes (Hammock & Johnson, 2014). However, contrary to this expectation, the negative effect of introduced predators was weaker in warmer lakes than in colder lakes.

Abiotic mechanisms

While previous studies have suggested potential abiotic mechanisms for a reduction in emerging abundance with warmer temperatures, we were largely able to rule out these factors and demonstrate little evidence for abiotic mechanisms. Specifically, factors such as hypoxia and changes in nutrient status, which can be directly related to water temperatures and stratification, and can determine the suitability of habitat for various insect taxa (Hogg & Williams, 1996), did not contribute to the results of this study. All six sites had similar low nutrient status, clear water column (Secchi depth at or near the benthos), and dissolved oxygen near or above saturation throughout daylight hours throughout the summer (Appendix S3), so variation in these parameters is unlikely to explain the patterns observed. In addition, a PCA of abiotic lake variables showed no significant portion of variance correlated to the presence of fish (Appendix S1: Figure S2).

Other field surveys conducted over large elevation gradients suggest that warmer (lower) lakes tend to have more habitat structure (largely terrestrial detritus) or more extensive shallow areas, meaning that more refugia are available for prey taxa to avoid predation (Knapp et al., 2001; Piovato-Scott et al., 2016). However, no major differences in substrata, area of shallows, or structure were observed between the six lakes in this study (Appendix S4). Furthermore, if habitat structure were a major factor, then it should have also led to

differences in non-Dipteran abundance across the temperature range, as those larger bodied insects are more vulnerable to predation. No such trend was observed in this study.

Trophic mechanisms

Indirect explanations for reduced emergence in warmer lakes include temperature-driven changes to interspecific dynamics such as predation and competition. We found no evidence of support for increased predation, but some evidence for increased competition, in warmer lakes. To rule out the hypothesis that predator compensation—that is, nontrout predators that would also exert top-down control on insect populations—reduced overall insect abundance as well as the relative effect of fish presence, we used data from the Sierra Lakes Inventory Project dataset (Knapp et al., 2020), discussed in Appendix S2. This analysis revealed that most amphibian predators of invertebrates should be less common in warmer lakes. Therefore, predator compensation is not likely to explain our findings.

Our data provide limited support for the hypothesis that reduced abundance in warmer lakes could be due to within-lake competition between Diptera larvae and other grazers. Some zooplankton grazers, such as rotifers and copepods, are more common at lakes lower within this elevation range (Appendix S2: Figure S1) while benthic algae and detritus had no significant variation with lake temperature in our study (Appendix S4). This could mean that less food is available to Diptera larvae, reducing the overall survival and emergence probability of subsidy vectors. However, this explanation is not well supported by the body size data collected. Starvation should have led to reduced individual body sizes as well as abundance. Instead, warmer lakes contained Diptera with larger average bodies (Figure 2B). Because Diptera were not identified to species, whether the changes in body size were due to a compositional shift or to a change in adult body size within each species is not knowable within the scope of this project. However, the shift in mean body size observed across temperatures (from <1 to 8 mm) would be improbable within species, indicating that we may have captured a shift in species prevalence.

CONCLUSIONS

We found that an additional 3.6°C of water temperature in oligotrophic alpine lakes was associated with a significant reduction in insect emergence, an increase in Diptera body size, and a reduced impact of predator

presence on insect emergence. Our results suggest that these effects are more likely to stem from changes in predator behavior and habitat use than from metabolic, abiotic, or trophic mechanisms.

Studies of interacting stressors need to account for behavioral and spatial effects that may be challenging to recreate in mesocosms. Additionally, insect population size structure is known to affect subsidy transfer from lake and stream systems (Jonsson et al., 2015; McKie et al., 2018; Stenroth et al., 2015). Given the importance of insect subsidies and the relevance of their size structure, further work is needed to understand the effects of temperature on insect population size structure across systems. To provide the greatest benefit to emerging insects and the linked systems that rely on them, these results suggest eradication of introduced trout should be prioritized in habitats that will remain relatively cool under future climate scenarios. More generally, protection of climate refugia should to whatever extent possible account for resistance to multiple types and scales of change.

While our findings are specific to oligotrophic alpine lakes, our conclusions also have global and forward-looking relevance. This study contributes to a detailed body of knowledge on interacting stressors and extends our understanding of impacts to ecosystems that serve as sentinels of global change. Furthermore, we expect that with increasing variability in snowpack forecasted, Sierra lakes will experience more warm years in the future—as will freshwater systems worldwide, whose temperatures are rising as much as two times faster than air temperatures (O'Reilly et al., 2015). This work adds to our understanding that protecting threatened populations, such as insect populations that are experiencing declines worldwide, will require the simultaneous management of both local- and global-scale stressors as well as consideration of behavioral patterns.

ACKNOWLEDGMENTS

Fieldwork for this study was conducted on unceded homelands of the Mono and Northern Paiute people, under permits from California Dept. of Fish and Wildlife (SC-12998) and Sierra National Forest (HSD1333). Many scientists contributed to the collection of field data for this manuscript, including Anne Bilse, Kathryn Culhane, Jagger Joyner, Tiger Lao, Thomas Lenihan, Michael Maniscalco, Yadi Galindo Salazar, Chelsea Steel, Asher Thompson, Charlie Thrift, Donica Washington, and Wilma Wei. Nuzha Baksh, Madeleine Pacheco, and Emily Wapman assisted with sample processing. The manuscript was greatly improved thanks to the attention and edits of John Melack, Tom Smith, and Jennifer King.


CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and novel code (Owens et al., 2023) are available from Dryad: <https://doi.org/10.25349/D9QW5X>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Owens, Caroline H., Michelle J. Lee, Melissa Grim, John Schroeder, and Hillary S. Young. 2023. "Interactions between Temperature and Predation Impact Insect Emergence in Alpine Lakes." *Ecosphere* 14(7): e4619. <https://doi.org/10.1002/ecs2.4619>