



Effects of increased temperature on arctic slimy sculpin *Cottus cognatus* is mediated by food availability: Implications for climate change

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Abstract

1. Lakes are vulnerable to climate change, and warming rates in the Arctic are faster than anywhere on Earth. Fishes are sensitive to changing temperatures, which directly control physiological processes. Food availability should partly dictate responses to climate change because energetic demands change with temperature, but few studies have simultaneously examined temperature and food availability.
2. We used a fully factorial experiment to test effects of food availability and temperature (7.6, 12.7, and 17.4°C; 50 days) on growth, consumption, respiration, and excretion, and effects of temperature (12 and 19.3°C; 27 days) on habitat use and growth of a common, but understudied, mid-level consumer, slimy sculpin *Cottus cognatus*, in arctic lakes. We also used bioenergetics modelling to predict consumptive demand under future warming scenarios.
3. Growth rates were 3.4x higher at 12.7°C in high food compared to low food treatments, but the magnitude of differences depended on temperature. Within low food treatments, there was no statistical difference in growth rates among temperatures, suggesting food limitation. Consumption, respiration, and nitrogen excretion increased with temperature independent of food availability. Lower growth rates coincided with lower phosphorus excretion at the highest temperature, suggesting that fish selectively retained phosphorus at high temperatures and low food. In habitat choice experiments, fish were more likely to use the 12°C side of the tank, closely matching their optimal temperature. We predicted a 9% increase in consumption is required to maintain observed growth under a 4°C warming scenario.
4. These results highlight considering changes in food resources and other associated indirect effects (e.g. excretion) that accompany changing temperatures with climate change. Depending on how food webs respond to warming, fish may cope with predicted warming if density-dependent feedback maintains population sizes.

KEYWORDS

bioenergetics, ecosystem effects, excretion, lakes, trophic resources, warming

1 | INTRODUCTION

Predicting the responses of consumers, such as fishes, to climate change requires an understanding of how temperature changes influence consumer demand and resource availability. Aquatic consumers, such as fishes, are especially vulnerable to climate-mediated changes to the environment because they are ectothermic and confined to aquatic habitats (Ficke, Myrick, & Hansen, 2007; Sandblom et al., 2016; Whitney et al., 2016). The relative effects of warming on consumer demand versus resource availability will probably partly dictate the nature of the response (i.e. positive, negative, or neutral) at higher levels of organisation (i.e. populations, communities, ecosystems). Imbalances between an individual's energetic and nutritional demand and the availability of resources may cause population collapses and substantial changes to food web structure and functioning (Budy & Luecke, 2014; Durant et al., 2007; Winder & Schindler, 2004). Fish physiological processes are directly controlled by ambient water temperature, and increases in temperature lead to increased metabolic rates, such as consumption, excretion, and respiration (Clarke & Johnston, 1999; Hill & Magnuson, 1990; Vanni & McIntyre, 2016). Consequently, changes in the thermal environment lead to changes in their performance (e.g. growth, survival; Ficke et al., 2007; Huss et al., 2019; Whitney et al., 2016). Consumer responses to climate change will not only depend on the direct impacts of temperature changes, but also on indirect effects such as food availability in general and food availability versus increased consumer demand (Hill & Magnuson, 1990; Hury & Benstead, 2019). However, this latter point has received relatively less attention in studies predicting the effects of global climate change on fishes (but see Breeggemann et al., 2016; Kao et al., 2015), which have primarily focused on range shifts in response to changing temperatures (reviewed in Krabbenhoft et al., 2020; Lynch et al., 2016; Myers et al., 2017).

The Arctic is an ideal and important system to test for effects of changing temperature and food availability on consumers because it is warming faster than any other region on the globe (ACIA, 2005; Hobbie & Kling, 2014; IPCC, 2014), with an observed 2.7°C increase in average air temperature over the past 4 decades (Box et al., 2019). For context, this rate of warming is 2.4× faster than for the rest of the Northern Hemisphere, and even more dramatic increases are projected over the next 100 years (US EPA, 2012). Arctic ecosystems are predicted to be sensitive to the effects of global climate change (Poesch et al., 2016; Prowse et al., 2006; Reist et al., 2006), and lakes in particular are extremely sensitive to the surrounding climate and can rapidly respond to change (Adrian et al., 2009; Schindler, 2009). For example, inland lakes may be warming twice as fast as local air temperatures, and are experiencing later freezing and/or earlier break-up of ice cover (MacIntyre et al., 2009; Magnuson et al., 2000; Schneider & Hook, 2010). Further, climate change is considered a major driver of the disappearance of about half of the lake area in a region of northern China (Yang & Lu, 2015), the increased nutrient loading in European lakes (Jeppesen et al., 2011), and shifting species distributions and biodiversity in

Canadian lakes (Alofs et al., 2014). These effects exemplify climate change consequences occurring in freshwater systems worldwide, resulting in altered ecosystem processes and structure, and affecting ecosystem services and national economies (Allison et al., 2009; Grimm et al., 2013; Woodward et al., 2010).

The responses of arctic lake systems to climatic warming are an understudied topic, and thus, their responses remain uncertain (Post et al., 2009). Lakes in the Arctic are comprised of simple food webs with low species diversity (Hershey et al., 1999), making them favourable systems to study, due to the low number of complex interactions. Arctic lakes are also largely devoid of direct anthropogenic impacts (e.g. land use change) and as a result, these lakes are ideal for teasing apart the effects of climatic warming in the absence of confounding anthropogenic factors. Further, arctic lakes hold both social and economic importance for local communities (White et al., 2007), as many arctic communities rely heavily on lakes for subsistence (Moerlein & Carothers, 2012; Pedersen & Hugo, 2005). Therefore, from an ecological and social perspective, it is necessary to understand how arctic lake food webs will respond to a warming climate.

Slimy sculpin *Cottus cognatus* are an important prey resource for top predators in arctic lakes, such as Arctic char *Salvelinus alpinus* (Hershey et al., 1999; McDonald & Hershey, 1992), but they are understudied relative to other arctic fishes. Slimy sculpin (sculpin hereafter) are an important mid-level consumer; providing a link between benthic and pelagic compartments of the food web. Sculpin occur in streams and lakes across northern portions of North America and Siberia, including broad distribution throughout Alaska, U.S.A. and Canada. Sculpin from arctic habitats grow slower and live longer (8+ years) than more southerly populations (McDonald et al., 1982), and may be food limited in these systems (Hershey & McDonald, 1985). In arctic lakes, these fish primarily occupy nearshore littoral zones near the rock-sediment interface; however, individuals may be found anywhere from shore to 7 m deep (Hershey, 1985; McDonald et al., 1982). Because sculpin live primarily in the epilimnion, the warmest zone of the lake, the effects of climate change might be severe for sculpin in small arctic lakes because their restriction to the shallow littoral zone limits access to regulate their thermal preference, unlike more pelagic arctic fishes, such as Arctic char or lake trout *Salvelinus namaycush*.

Our goal was to test the coupled effects of warming and food availability on growth and physiological performance of sculpin from arctic lakes. We tested the effects of simulated climate warming and food availability on rates of growth, consumption, and excretion of sculpin in a laboratory setting. Because most arctic fishes are currently occupying water temperatures less than their optimum for growth and consumption, based on basic metabolic principles of ectotherms (Kitchell et al., 1977), we predicted sculpin would exhibit higher growth rates near their optimum temperature, and growth rates would be lower at both colder and warmer temperatures. In addition, the nature and extent to which sculpin physiological performance is altered by warming should be modulated by food availability. That is, we expected to find an interaction

between temperature and food availability where growth would decrease with increasing temperatures, but more so in conditions of lower food availability. Also, we evaluated the behavioural response of sculpin to warming conditions by conducting a thermal habitat choice experiment, and predicted that sculpin would select habitats closest to their optimum temperature. Finally, we used bioenergetics modelling to predict consumptive demand under scenarios of future climate warming.

2 | METHODS

2.1 | Study area

Our research was conducted in lakes near Toolik Field Station (TFS; 68°37.796'N, 149°35.834'W), home of the Arctic Long Term Ecological Research project (<http://arc-lter.ecosystems.mbl.edu/>), in the northern foothills of the Brooks Mountain Range, Alaska (Figure 1a).

2.2 | Study design

2.2.1 | Temperature and food availability

To test the effects of temperature and food availability on sculpin, we conducted a fully factorial experiment exposing fish to three temperature treatments (7.6, 12.7, and 17.4°C) crossed with two food availability treatments using previously frozen and thawed chironomid larvae as prey (0.07 and 0.27 g fish⁻¹ day⁻¹; Figure 1b). Chironomids are the primary food resource for sculpin in arctic lakes (Hershey & McDonald, 1985). We chose treatments based on published data on thermal preferences and feeding rates of the species (Hershey, 1985; Otto & Rice, 1977; Symons et al., 1976), with optimal temperatures reported to be 9, 12, and 13°C at acclimation temperatures of 5, 15, and 20°C, respectively, and feeding rates of 13.4 chironomids/day. The 7.6 and 12.7°C temperatures are also representative of summer temperatures in Lake Fog1, while the 17.4°C temperature is representative of potential warming (Table 1). We replicated each treatment combination twice. We inoculated

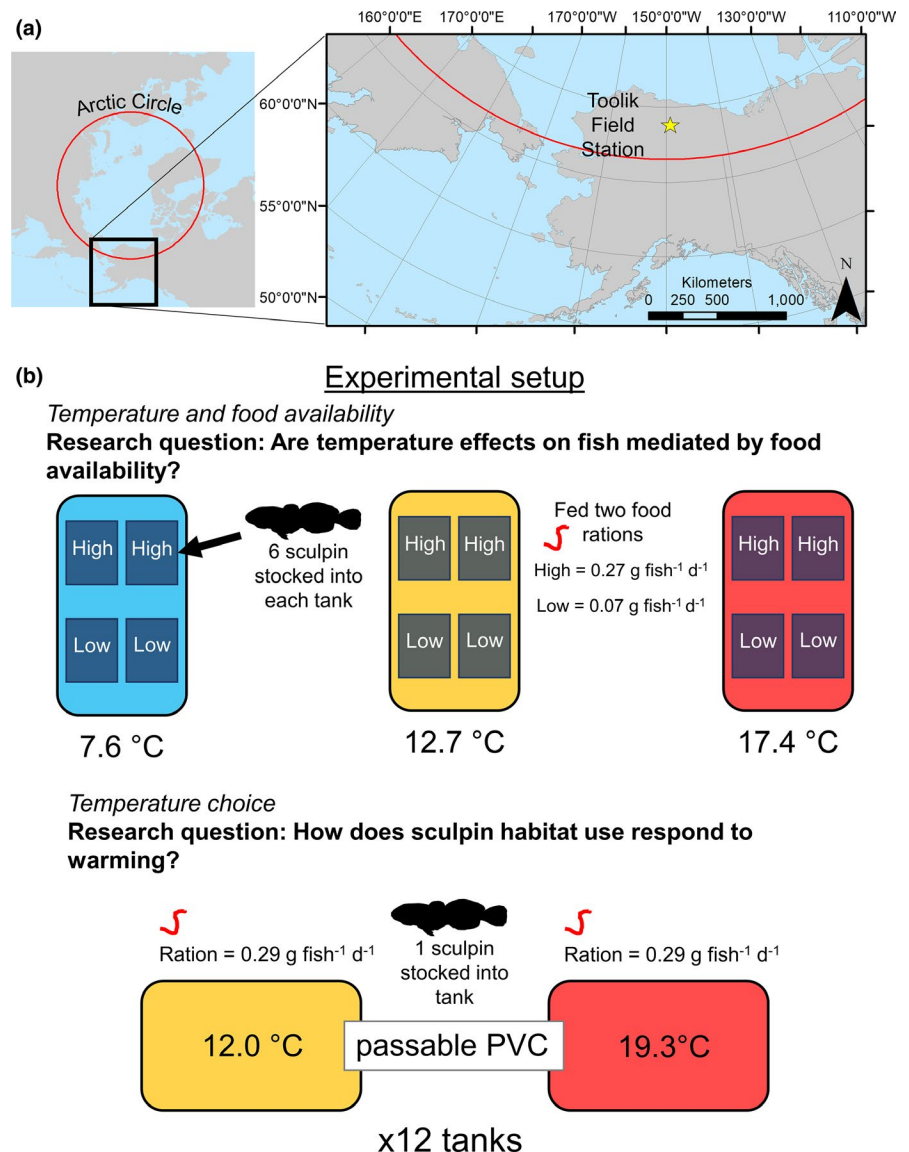


FIGURE 1 (a) Toolik Field Station, Alaska, is located on the north slope of the Brooks Range. (b) Conceptual figure of our experimental set up and research questions. These experiments allowed us to test for direct and indirect effects of climate change by manipulating temperature and food availability. We measured growth rates and physiological processes in the temperature and food availability experiment, and growth rates and consumption coupled with habitat use in the temperature choice experiment

TABLE 1 July water temperatures from 5 m depth in Lake Fog1 near Toolik Field Station, Alaska

Year	Minimum temperature (°C)	Mean temperature (°C)	Maximum temperature (°C)
2014	7.9	9.7	11.6
2015	10.9	12.9	14.6
2016	7.4	10.1	12.2
2017	7.1	10.3	14.4
2018	4.7	9.6	12.7

12 experimental tanks (40 L) with water from a nearby lake (Toolik Lake), and stocked six sculpin of similar size into each tank from the same lake. Sculpin collected from lakes near TFS typically range in size from 14 to 95 mm total length (mean = 50.6) and from 0.2 to 8.1 g (mean = 1.4 g; P. Budy, unpublished data). Fish weight (g) at the onset of the experiment did not differ among tanks (mean \pm SE, 0.74 ± 0.04 ; $p > 0.05$). Five fish expired during the experiment, and we replaced these with similar sized individuals to maintain densities. We excluded these individuals from analyses. The primary response variable was specific growth rate (SGR), which we calculated as:

$$\text{SGR} = \left[\frac{(\ln W^2 - \ln W^1)}{t^2 - t^1} \right] \times 100.$$

where W^1 and W^2 were body weight at the start and end of the experiment, respectively, and $t^2 - t^1$ was the length of the experiment in days. We ran the experiment for 50 days. To match conditions in nearby lakes, we covered the bottom of tanks with a mixture of soft and coarser, gravel-sized sediments, larger rocks, and submerged vegetation collected from nearby lakes. We immersed tanks in water baths that were heated using aquarium heaters, and continuously monitored temperatures with HOBO pendant loggers (UA-001-08; Onset Computer Corporation).

Additionally, we conducted individual-based trials of consumption, respiration, and excretion (nitrogen and phosphorus). To estimate temperature effects on consumption, we held individual fish, of similar sizes used in the growth experiment, in tanks within water baths matching the three temperature treatments above. We tested four fish per temperature. We fed fish ad libitum and measured consumption over several days for a total of 17 observations per fish. We quantified consumption by counting the number of food items consumed for each fish per unit time, and reported consumption on a per capita basis as g of prey consumed g of fish⁻¹ day⁻¹.

We used fish from the growth experiment to also measure the effects of temperature and food availability on respiration and excretion. Trials were conducted at the end of the experimental period. We measured individual respiration by placing individuals in 600–650 ml of water in sealed plastic containers and recording the change in dissolved oxygen over an approximately 2 hr period using a dissolved oxygen meter (HQ30D; Hach). We also measured background respiration in control chambers, which contained water only

(e.g. Rodgers et al., 2016), but observed no change over time. Similar to consumption, we report individual respiration on a per capita basis (mg O₂ g of fish⁻¹ hr⁻¹). Finally, we measured individual fish excretion by placing fish in 1-L containers with 700 ml of filtered water (GF/F; 0.7 μ m pore size; Whatman) and incubated in temperature baths matching their experimental treatment for at least 1 hr. We collected water samples at the end of each trial, and these were kept frozen until analyses at the University of Alabama. We analysed samples for NH₄⁺ (hereafter N) with the phenol method (ASTM, 2012) and soluble reactive phosphorus (hereafter P) with the colorimetric method (Murphy & Riley, 1962) using a Seal AQ300 discrete analyser (Seal Analytical). We calculated individual excretion rates as the difference in nutrient concentration between containers with sculpin and control containers without fish (e.g. Atkinson et al., 2013; Hopper et al., 2020).

2.2.2 | Thermal habitat choice

To measure temperature selection by sculpin, we connected two 5.7-L tanks with a PVC pipe that was passable by sculpin ($n = 12$ tanks). We heated one side of the tank to 12°C and the other to 19.3°C using aquarium heaters. As described above, we inoculated tanks with water, substrate, and vegetation from nearby Toolik Lake. We stocked one fish into each set of tanks and allowed them to freely move among sides. We introduced equal amounts of food to both sides of the tank at least once daily throughout the experimental period (i.e. 27 days). Throughout the experiment, we observed fish in the tanks and recorded which side fish were on, including if the fish was in the PVC pipe. We also recorded consumption in each side of the tanks by counting the number of chironomids remaining after each feeding bout.

2.3 | Data analysis

2.3.1 | Temperature and food availability

For analysis of SGR, we used individual fish as replicates ($n = 67$) in models including additive effects of temperature, food availability, and their interactive effect. We included tank as a random effect in models to account for the fact that individual fish from the same treatment are not independent samples. We inspected residual plots, which suggested heterogeneity of residuals among temperature treatments. Thus, we modelled variance by including the *varIdent* statement in the model, using temperature treatment as the stratum. We used the *lme* function in the nlme package to build models (Pinheiro et al., 2020). We tested for differences ($\alpha = 0.05$) in means of our response variables among treatments in all models using likelihood ratio tests (LRT) with the ANOVA function in the car package in Program R version 3.6.3 (Fox & Weisberg, 2019; R Core Team, 2020). Although LRT can be anticonservative, they typically outperform Wald's tests (Luke, 2017); we were limited in approaches

to test fixed effects, because we needed to account for heteroskedasticity within some of our models. We used the effects package to calculate marginal means and 95% confidence intervals (Fox & Weisberg, 2019), and the emmeans package was used for post hoc analyses with p -values corrected for multiple testing using Tukey's HSD (Lenth, 2020).

To test the effect of temperature on individual consumption ($n = 12$), we used a linear mixed effects model including temperature as a fixed effect and a random effect of observation to account for repeated measures of individuals. We modelled variance as described above. We used the *lme* function in the nlme package to build mixed models. We also used a linear mixed effects model to test for additive effects of temperature, food availability, and their interactive effect on respiration rate ($n = 48$) and excretion rate ($n = 36$), including tank as a random effect. We again inspected residual plots, and observed no indication for a need to model variance for respiration or excretion rates.

2.3.2 | Thermal habitat choice

To test whether sculpin preferred different temperatures, we analysed data in two different, but complementary ways. First, we tested if fish were found more often on one side of the tank than the other. We used presence-absence data based on observations of fish on the 12 and 19.3°C sides of the tank as a response variable in a generalised linear mixed effects model. We used temperature as a fixed effect and included a random effect of tank. We assumed a binomial distribution (link = logit). Additionally, we treated the observed temperature choices, including the PVC pipe, as encounter histories for each fish. For each observation period, if a fish was located in the 12°C side of the tank, it received a 1 in the column for 12°C and a zero for 19.3°C and the pipe. Using these encounter histories ($n = 65$ observation periods), we estimated transition probabilities among the three habitats given a fish's previous recorded location (L_t). We assumed fish moved among the three habitats randomly with transition probabilities D :

$$L_t = \begin{bmatrix} I_{1t} \\ I_{2t} \\ I_{3t} \end{bmatrix}$$

$$D = \begin{bmatrix} p_{11} & p_{12} & p_{13} \\ p_{21} & p_{22} & p_{23} \\ p_{31} & p_{32} & p_{33} \end{bmatrix}$$

$$L_{t+1} = DL_t$$

where L_t was a vector of the probabilities I_{it} of a fish being located in each habitat i at time t , D was the transition matrix containing probabilities p_{jk} indicating the probability of a fish transition from

habitat j to habitat k each time step. We assumed the observed locations at each time step t were multinomially distributed around L_t :

$$\ln \mathcal{L}(\hat{L}_t | \theta) = \sum_i n_{it} \ln(p_{it})$$

where \hat{L}_t was a vector of the number of fish observed in each habitat at time t , n_i was the number of fish observed in habitat i at time step t , and θ was a vector of all parameters estimated in the model. We estimated parameters with maximum likelihood using the bbmle package (Bolker & R Development Core Team, 2020).

2.4 | Bioenergetics modelling

Finally, we used the Wisconsin bioenergetics model to predict growth of sculpin under our experimental conditions and the potential impact of future climate scenarios on sculpin consumption in a manner complimentary to our experimental results. We ran models using Fish Bioenergetics 4.0 in R (Deslauriers et al., 2017). We parameterised models using data collected on prickly sculpin *Cottus asper* (Moss, 2001). However, we modified temperature parameters to better reflect temperature preferences of sculpin, and assumed an optimal temperature of 11°C (Otto & Rice, 1977; Symons et al., 1976). We assumed a diet consisting entirely of macroinvertebrates because chironomids are the primary prey base of sculpin in our study system (Cuker et al., 1992; Hershey, 1985; Hershey & McDonald, 1985). We also assumed diet energy densities were constant over time (3,000 J/g), and used energy densities for age-1 sculpin to match sizes of sculpin used in our experiments (4,317 J/g; Moss, 2001). To predict growth under our experimental conditions, we fit models to daily ration (low or high) across the three temperatures used in the experiment. We predicted growth using the initial weights of individuals used in the experiment within each treatment ($n = 67$), and calculated SGR as above. To investigate potential impacts of future climate scenarios on sculpin consumption, we fit models to observed growth rates of fish ($n = 23$) from the 12.7°C treatment in the first experiment and extrapolated these to a typical summer season (108 ice-free days) experienced by fish in Lake Fog1 at TFS and used temperature data from Lake Fog1 in 2016 taken at a depth of 5 m as a *baseline*. We assessed several warming scenarios based on climate projections for the Arctic including a 2 and 4°C increase (IPCC, 2014). We also ran scenarios where we assumed sculpin would behaviourally thermoregulate their position in the water column to optimise their temperature occupied (e.g. Busch et al., 2012; Habary et al., 2017). That is, we assumed that if optimal temperatures were available within the water column, then sculpin would occupy those temperatures. We restricted fish thermal position between 1 and 7 m deep, where DO levels are above 4 mg/L. Within the remaining habitat, we assumed sculpin would occupy waters closest to their optimal temperature for growth (11°C; Otto & Rice, 1977; Symons et al., 1976). We report the effect of climate warming in terms of the percent difference between the estimate of

total consumption from *baseline* and estimates from each warming scenario.

3 | RESULTS

3.1 | Temperature and food availability

Effects of temperature on sculpin were mediated by food availability (Figure 2). Sculpin from the higher food availability treatments grew faster, on average, compared to fish from the lower food availability treatments, but the magnitude of difference was dependent on temperature treatment (interaction term: $\chi^2 = 11.79$, $df = 2$, $p = 0.003$). Specifically, fish from the higher food treatments had a 1.8 \times , 3.4 \times , and 1.7 \times higher average SGR than fish fed less food in the 7.6, 12.7, and 17.4 $^{\circ}\text{C}$ temperature treatments, respectively. Differences in SGR between high and low food availability treatments were statistically significant within the 7.6 and 12.7 $^{\circ}\text{C}$ treatments (Tukey's HSD: $p < 0.010$), but not within the 17.4 $^{\circ}\text{C}$ treatment ($p = 0.115$). Across the higher food availability treatments, SGR was higher in the 12.7 $^{\circ}\text{C}$ compared to the 7.6 $^{\circ}\text{C}$ treatment ($p = 0.006$), but there was no significant difference between either the 12.7 and 17.4 $^{\circ}\text{C}$ treatments ($p = 0.127$) or the 7.6 and 17.4 $^{\circ}\text{C}$ treatments ($p = 0.601$). There was no significant effect (all $p > 0.323$) of temperature on SGR for fish fed the lower food availability. Variability in SGR was relatively higher in the 17.4 $^{\circ}\text{C}$ treatment in both food availability treatments (Figure 2a).

Individual consumption rates increased with temperature (LRT: $\chi^2 = 99.60$, $df = 2$, $p < 0.001$) and sculpin consumed at rates 1.7 \times higher in the 12.7 and 17.4 $^{\circ}\text{C}$ compared to the 7.6 $^{\circ}\text{C}$ treatment (Table 2). Respiration rates increased in a similar fashion with increasing temperature (LRT: $\chi^2 = 7.03$, $df = 2$, $p = 0.030$; Figure 2b).

The effect of food and the interactive effect of food and temperature were not statistically significant ($p > 0.493$). As with respiration rates, nitrogen excretion rates increased with temperature (LRT: $\chi^2 = 8.38$, $df = 2$, $p = 0.015$; Table 2), but were not significantly impacted by food availability or the interactive effect of food and temperature (both $p > 0.32$). There was a weak effect of the interaction between temperature and food on phosphorus excretion rates (LRT: $\chi^2 = 6.07$, $df = 2$, $p = 0.048$; Figure 2c), whereby rates were lowest in the 17.4 $^{\circ}\text{C}$ when food availability was low, but highest when food was high. Consequently, N:P demonstrated a similar pattern as phosphorus excretion with a weak interaction between temperature and food (LRT: $\chi^2 = 5.47$, $df = 2$, $p = 0.065$; Figure 2d).

3.2 | Thermal habitat choice

In the thermal habitat choice experiment, sculpin were more likely, on average, to be observed on the 12 $^{\circ}\text{C}$ side of the tank relative to the 19.3 $^{\circ}\text{C}$ side (LRT: $\chi^2 = 49.66$, $df = 1$, $p < 0.001$; Figure 3a). Despite a 7 $^{\circ}\text{C}$ temperature difference between sides of the tank, individual sculpin were observed on the 19.3 $^{\circ}\text{C}$ side during 4–86% of the observation periods. Fish were also observed in the PVC tube connecting the two sides of the tank 22% of the time. With regard to transitioning among sides of the tank (or the pipe), sculpin were nearly twice as likely to move towards the 12 $^{\circ}\text{C}$ side, from either the pipe or the 19.3 $^{\circ}\text{C}$ side, than away from the 12 $^{\circ}\text{C}$ side (Figure 3b). Estimates of transition probabilities suggested fish were most likely to remain in the habitat where they were last observed. Differences in observed temperature use had no bearing on consumption in either side of the tank. Specific growth rates of individual sculpin ranged from 0.96% to 5.37% (mean \pm SD; 2.16 ± 1.10). The proportion of time observed in the 12 $^{\circ}\text{C}$ side of the tank was not significantly related to individual

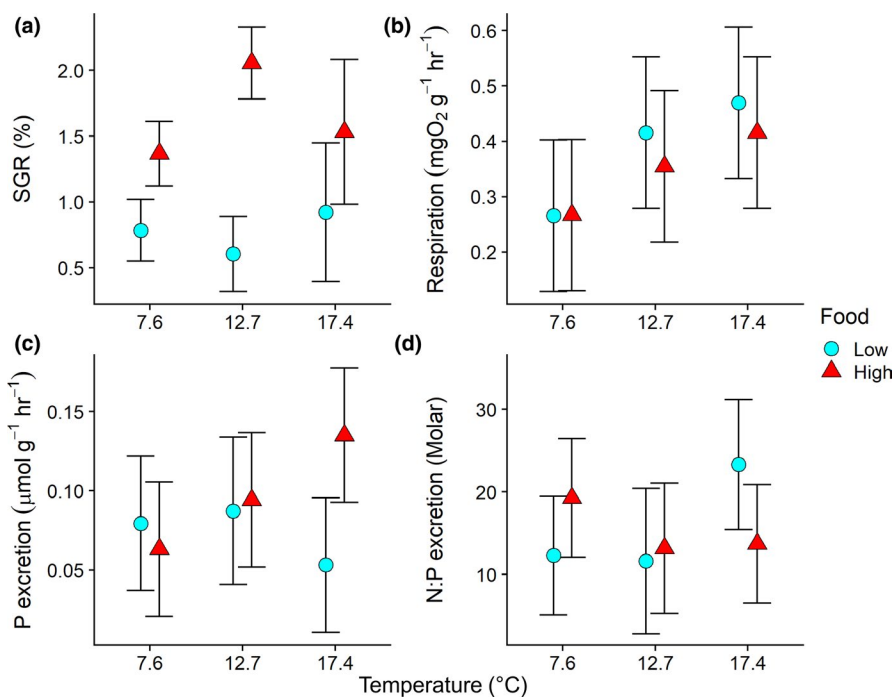


FIGURE 2 Marginal mean (\pm 95% confidence intervals) estimates of (a) specific growth rates (SGR), (b) respiration, (c) P excretion, and (d) N:P excretion of slimy sculpin ($n = 52$) from crossed treatments of temperature and food availability. There was a significant interaction between food availability and temperature treatments for SGR ($p = 0.003$) and weaker interactions for P excretion ($p = 0.048$), and N:P excretion ($p = 0.065$). Respiration increased significantly with temperature ($p = 0.030$)

TABLE 2 Mass-specific rates of consumption, respiration, and excretion of slimy sculpin exposed to varying temperature and food availability treatments

	n	Temperature		
		7.6°C	12.7°C	17.4°C
Consumption rate (g g ⁻¹ day ⁻¹)	12	0.26 (0.03)	0.48 (0.05)	0.44 (0.04)
Respiration rate (mg O ₂ g ⁻¹ hr ⁻¹)	48			
Low food		0.27 (0.02)	0.42 (0.03)	0.47 (0.07)
High food		0.27 (0.03)	0.35 (0.02)	0.42 (0.04)
Excretion rate (μmol g ⁻¹ hr ⁻¹)	36			
Nitrogen				
Low food		0.77 (0.11)	0.90 (0.16)	1.12 (0.13)
High food		0.82 (0.15)	1.10 (0.15)	1.23 (0.12)
Phosphorus				
Low food		0.08 (0.01)	0.09 (0.01)	0.05 (0.01)
High food		0.06 (0.02)	0.09 (0.02)	0.14 (0.04)
N:P (Molar)				
Low food		12.29 (3.27)	11.62 (0.69)	23.29 (4.72)
High food		19.25 (3.85)	13.17 (2.96)	13.70 (4.13)

Note: Values are mean (SE).

SGR ($p = 0.275$). Per capita consumption did not differ among sides of the tank ($p = 0.393$), suggesting fish were moving among sides to feed and consuming similar number of chironomids on both sides ad libitum.

3.3 | Bioenergetics modelling

Predicted growth rates of sculpin fed rations and held at temperatures matching our experiment were consistently higher than we observed in our experiment. Specific growth rates from modelled predictions were higher for fish fed higher rations regardless of the temperature regime, based on non-overlapping 95% confidence intervals (Figure 4a). Based on bioenergetic models, we predicted sculpin consumption during the ice-free period must increase at least 5% and as much as 9%, depending on warming and fish behavioural response scenarios, to maintain current summer growth (Figure 4b). For the baseline temperature regime, 8.3 g of invertebrate prey were required to achieve observed growth of an average size fish during the 108 days growth period. We predicted consumption to be highest under the +4°C warming scenario with a predicted consumption of 9.0 g of an average size fish. The effects of behavioural thermoregulation were also predicted to be highest in the +4°C warming scenario, where the difference in total consumption between thermoregulating and not was about 19% for an average size fish.

4 | DISCUSSION

Climate change effects on fishes are rarely considered within the context of food availability. Our experimental and simulation results

suggest fish in arctic lakes might be able to cope with predicted warming scenarios if there is enough invertebrate production to compensate for increasing metabolic demands, and if density-dependent feedback controls population size (Budy & Luecke, 2014). Slimy sculpin in arctic lakes are slower growing compared to more southerly populations (McDonald et al., 1982), and our estimates of consumption suggested they require relatively minimal daily rations (0.04 g/day) to grow at current lake temperatures. This could have contributed to differences between predicted growth rates from the bioenergetics model and our observed growth rates (Bajer et al., 2004); although we assumed a constant ration, we lack precise estimates of food consumed in our experiment. The magnitude of increase in food availability required in the wild will probably depend on the ability of fishes to behaviourally thermoregulate (Busch et al., 2012), which could be impacted by changes in stratification patterns in lakes. Fish in our experiment demonstrated the behavioural capacity to adjust to changing temperatures, and some individuals spent substantial time in habitats that were 8°C warmer than their laboratory-measured optimal of 11°C (Otto & Rice, 1977). However, future warming is predicted to deepen the epilimnion in arctic lakes, potentially causing a temperature–oxygen squeeze through simultaneous warming of the epilimnion and de-oxygenation of the hypolimnion (Butcher et al., 2015; Ficke et al., 2007; Jones et al., 2008). This physical change to the lake environment could ultimately reduce the amount of suitable habitat in particular for littoral, benthic fishes (Magnuson et al., 1979).

Consumption is temperature-dependent in fishes and whether increases in temperature within the habitable thermal limits of a species will be beneficial or detrimental to fish production will ultimately depend on how food resources respond (Hill & Magnuson, 1990; Kitchell et al., 1977). Generally, aquatic ecosystems in the Arctic

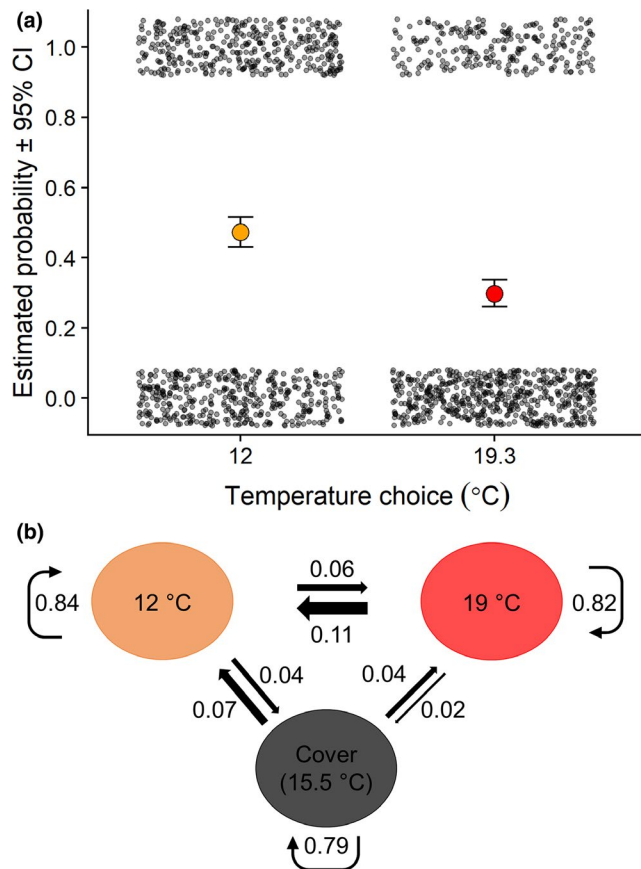


FIGURE 3 (a) Sculpin tended to be observed more often in the 12°C habitat (LRT: $\chi^2 = 49.66$, $df = 1$, $p < 0.001$). (b) Given their last observed location, sculpin were most likely to remain in the same habitat, and were nearly twice as likely to move towards the 12°C habitat, from either the PVC pipe (cover) or the 19.3°C habitats, than away from the 12°C habitat. Width of arrows among habitats is proportional to the estimated transition probability

are predicted to become more productive with future warming (Levine & Whalen, 2001; Prowse et al., 2006; Vucic et al., 2020). For instance, zooplankton biomass is expected to increase in arctic lakes with increases in temperature and longer ice-free periods (Klobucar et al., 2018), and these predicted increases fall within the range of increased consumptive demand predicted for fish species, such as Arctic char (Budy & Luecke, 2014). Additionally, growth rates of chironomids, the main prey source of slimy sculpin in arctic lakes, increase with temperature and peak near 20°C (Reynolds & Benke, 2005). Together, these studies suggest food resources might respond positively, and potentially with enough magnitude, to compensate for increased fish consumption at warmer temperatures in arctic lakes, but this will also depend on how food resources of primary consumers respond to climate change. Moreover, other controls on aquatic productivity in the Arctic, such as low nutrients, light limitation from dark winters, and increases in turbidity could limit fish productivity (Huryn & Benstead, 2019; Levine & Whalen, 2001; van Dorst et al., 2019). Hence, monitoring the response of food resources to climate change at all trophic levels will be vital to assessing the realised impacts of climate change on lake food webs.

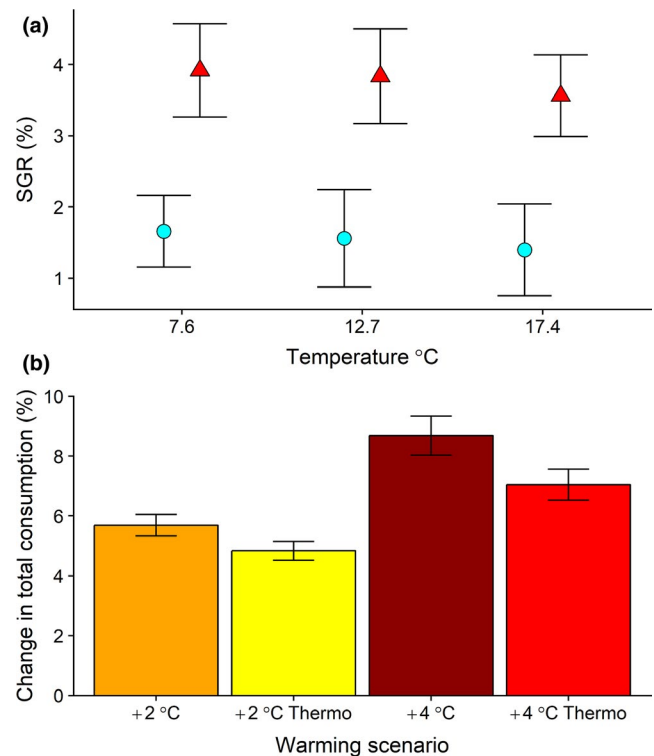


FIGURE 4 (a) Specific growth rates over 50 days based on predicted growth from bioenergetics models using temperature regimes from our experiment fit to daily rations (low = circles, high = triangles) and using initial fish weights ($n = 67$). Values are means and error bars are 95% confidence intervals. (b) Predicted difference (%) in consumption (g) by sculpin increased with warming relative to baseline temperatures. Values are means and error bars are 95% confidence intervals. We estimated consumption during a typical summer season (~108 days) with a bioenergetics model fit to final weight based on observed growth in fish ($n = 23$) from the 12.7°C treatment from the experiment testing effects of temperature and food availability. We ran warming scenarios assuming both static increases in temperature and allowing fish to behaviourally thermoregulate (Thermo). We used temperatures from a depth of 5 m from Lake Fog1 in 2016 at Toolik Field Station, Alaska, U.S.A., as the *baseline*

Future climate change could impact the ecosystem effects of fishes, both directly (excretion) and indirectly (consumption; Atkinson et al., 2017; van de Waal et al., 2010). Fish in our experiment demonstrated lower P excretion and higher N:P excretion in the highest temperature and low food availability treatments, which suggests that sculpin could selectively retain P at higher temperatures if food is limiting. Phosphorus limited growth is not uncommon in fishes (Benstead et al., 2014; Hood et al., 2005; Raubenheimer & Simpson, 2004), and lower consumption has been suggested to increase P retention efficiency by fish (Moody et al., 2018). Mass-specific rates of N and P excretion by sculpin in our experiments increased with temperature when food availability was high, but rates were lower than values reported for other co-occurring pelagic fish species in lakes near TFS (Johnson et al., 2010). However, their contributions to demand of primary producers might be higher based on estimated areal excretion

rates. For instance, using a biomass estimate of slimy sculpin from Lake Fog1 (P. Budy, unpublished data) and individual excretion rates from our experiments, N areal excretion of sculpin in Fog1 is approximately $0.01 \mu\text{g L}^{-1} \text{day}^{-1}$ and P areal excretion is approximately $0.002 \mu\text{g L}^{-1} \text{day}^{-1}$. Combined fish areal excretion from three species in a nearby lake (i.e. Fog2) of similar size as Fog1, was estimated to be 0.03 and $0.003 \mu\text{g L}^{-1} \text{day}^{-1}$ for N and P, respectively (Johnson et al., 2010). These excretion rates were estimated to contribute to 5.1% of N demand and 4.6% of P demand by producers. If we assume these levels of demand are representative of nearby lakes, slimy sculpin could contribute, a conservative, 2.5% of N and 3.3% of P demand, given their estimated population size and assuming the average size fish is 1.5 g. The indirect effects of fish on nutrient cycling are larger than their direct effects in arctic lakes because they substantially reduce zooplankton standing stocks (Johnson et al., 2010), and zooplankton contribute to 19–130% of N and 37–200% of P demand of primary producers. As temperatures warm and fish consumptive demands increase, fish effects on zooplankton could increase, and nutrient ratios of fish excretion could change, potentially altering nutrient cycling in these systems.

Ecosystems at high latitudes, such as those near TFS, are experiencing the fastest rates of warming on the globe (ACIA, 2005; Hansen et al., 2007; Hobbie & Kling, 2014), and it is not clear whether organism responses will keep pace with these quickly changing conditions (reviewed by Comte & Olden, 2017; Crozier & Hutchings, 2014). Predicting organism responses to climate change is made more difficult because results from studies comparing thermal adaptation between northern and southern populations of wide-ranging species are equivocal. For example, thermal tolerance was higher in southern than in northern populations of common killifish *Fundulus heteroclitus* regardless of acclimation temperatures (Fangue et al., 2006). In contrast, other studies suggest northern populations are more tolerant of high temperatures (e.g. Gaitán-Espitia et al., 2014; Yu et al., 2018), and even still, others have found no evidence for thermal adaptation among populations (reviewed in Elliot & Elliot, 2010). The climatic variability hypothesis (Levins, 1969; Stevens, 1989) predicts that individuals at higher latitudes have greater physiological plasticity, because they experience a broader range of temperature variation. If this were true, then fishes in the Arctic would be more likely to adapt to warming than more southern populations or species. Alternatively, local adaptation to average temperatures could mean that even small changes in temperature could have deleterious effects (Levington, 1983; Parmesan et al., 2005). There is evidence that arctic fishes have already experienced temperatures as much as 6°C warmer than present day within their evolutionary history (i.e. within the last 10,000 years; Axford et al., 2017; Nelson & Carter, 1987), and fish populations can respond rapidly to changes in selective pressures (e.g. Christie et al., 2016). This, together with results from our experiments, suggests slimy sculpin in arctic lakes can survive and grow under increased temperatures, and their adaptive capacity to warming will be aided by being able

to find suitable microhabitats (i.e. thermoregulation) and increases in food availability that keep pace with consumptive demand. However, as discussed above these microhabitats might not be available (e.g. Ficke et al., 2007).

Human-induced effects on Earth's climate have led to unprecedented rates of change in temperatures. Although it has been predicted to be unlikely that lakes will experience warming high enough to rapidly and directly harm fish populations (Elliot & Elliot, 2010), this outcome will depend on how global climate change impacts other variables of lake ecosystems, such as stratification, and whether suitable microclimates of temperature and oxygen are maintained within a range habitable to fishes (e.g. Sandblom et al., 2016). The resilience of freshwater ecosystems in the Arctic to climate change will probably be aided by a lack of additional human impacts that plague aquatic systems at lower latitudes, such as fragmentation and land use change (e.g. Comte & Olden, 2017). However, other disturbances that are increasing in frequency and magnitude associated with the direct effects of climate change include coarse-scale tundra fires (Hu et al., 2010, 2015; Mack et al., 2011) and thermokarst failures resulting in the mass transport of soil (turbidity), vegetation, and dissolved constituents (nutrients) into surface water (Bowden et al., 2008). It is not clear how these indirect effects will impact arctic lake systems through bottom-up effects. In arctic lakes, increases in temperature will likely be accompanied by longer growing seasons, increased productivity, changes in stratification patterns, and changes in species composition, which will have both direct and indirect effects on fishes. Future studies might consider more than just thermal preferences when assessing species' responses to climate change, but also consider other dimensions of a species' niche that are controlled by changes in temperature, such as food availability and food web stability.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

C.A.P. analysed the data and C.A.P. and P.B. led writing the manuscript. N.B., C.L.A., and P.B. collected the data and analysed samples. All authors contributed to ideas and editing of the final manuscript.

DATA AVAILABILITY STATEMENT

Long Term Ecological Research data are available at <https://arc-lter.ecosystems.mbl.edu/>. Experimental data are available from the authors upon request.

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