Warming and Predation Alter Consumer Coexistence

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Abstract

Understanding how species coexist is a key question in ecology, with implications for conserving biodiversity. Species coexistence is affected by multiple factors, including climate warming and the presence of predators, yet most studies consider these 'stressors' in isolation. The interactive effects of warming and predation on species coexistence have not been explored. Here, we constructed simplified shallow lake food webs in 24 large mesocosm ponds and applied a crossed design to simulate warming (+4.5°C) and predation (by crucian carp *Carassius auratus*). We monitored population responses of two common snails, *Bellamya aeruginosa* and *Radix swinhoei* over 200 days. We predicted that warming will alter the phenology of the snails, and that this will combine with predation to reduce their abundance. Warming advanced the reproduction of *R. swinhoei* by 21.5 days and reduced biomass and density of both snails. The advance in *R. swinhoei* phenology suppressed the slower growing *B. aeruginosa* population, reducing coexistence. Warming and predation combined in an additive manner to decrease the biomass of *B. aeruginosa*. In contrast, the two drivers synergistically decreased the biomass and density of *R. swinhoei* because of enhanced pressure from the fish on their preferred snail prey under warming, due to rising metabolic demands. Therefore, snail coexistence was further reduced with fish presence under warming. In conclusion, future continuous warming and strong predation might undermine the coexistence of the gastropods, thereby changing food web structures in shallow freshwater ecosystems.

Introduction

Understanding factors and processes that shape species coexistence is a central question in community ecology. The framework of modern coexistence theory has been widely used to clarify the conditions for species coexistence (Barabas et al. 2018; Chesson 2000, 2018; Pande et al. 2020), which points out the mechanisms of promoting species coexistence via minimizing average fitness differences (equalizing) and increasing niche differences (stabilizing) (Letten et al. 2017). Without niche differences, the species with higher average fitness will eventually exclude the others. However, all species coexistences occur in changing environments, temporally and spatially, as environmental variation promotes species coexistence (Chesson 1994; Kuang and Chesson 2008). To coexist, different species might respond nonlinearly to fluctuating limiting factors, or via storage effects, such as resource partitioning (Levine and HilleRisLambers 2009), differential vulnerability to predators (Chesson and Kuang 2008) or pathogens (Bagchi et al. 2014), occupation of different microhabitats (Schlägel et al. 2020; Silvertown 2004), or phenological separation (Usinowicz et al. 2017). However, our planet has been experiencing unprecedented changes due to anthropogenic activities (Steffen et al. 2015), yet it remains to be explored how this affects species coexistence and what the consequences of changes in coexistence are for entire ecosystems (Thakur et al. 2017).

Previous studies have demonstrated that the warming associated with climate change will alter phenology (Thackeray et al. 2016), distribution patterns (Parmesan and Yohe 2003), species interactions (Schaum et al. 2018; Zhang et al. 2020), and food web structure (O'Gorman et al. 2019; Schwarz et al.

2017). Climate warming can also affect species coexistence directly through physiological impacts or indirectly via alterations in food web interactions (Reuman et al. 2014). Indirect cascading effects via species interactions (e. g. phenological mismatch, changing in resource availability or predation) generally have greater impacts than direct ones (Ockendon et al. 2014). Temperature plays a key role because warming will change the vital rates of individuals, and species usually have limited thermal tolerance (Rohr et al. 2018; Sunday et al. 2012). There are two key mechanisms by which warming will alter coexistence: (i) shifting phenology and (ii) increasing metabolic demands. The first predicts that populations will differ in their temporal responses to warming: acclimation capacities to the changing temperatures will differ among (Pinsky et al. 2019; Rohr et al. 2018) and within (Dahlke et al. 2020) species. For instance, stenothermal species might be more sensitive to warming than eurythermal species (Dahlke et al. 2020; Pörtner et al. 2005), and early-season species might shift more in time than later-season species (Wolkovich et al. 2012). Therefore, warming might increase the phenological mismatch between coexisting species, thus reducing the degree of competition strength between them (Chmura et al. 2019) (Fig. 1, mechanism i). The latter mechanism refers to the greater metabolic demands which individuals experience at higher temperatures.

For ectothermic herbivores which share the same resource, warming should enhance competition, because ingestion rates of heterotrophs generally increase more rapidly with rising temperature than the growth rates in autotrophs (Grainger et al. 2018; O'Connor 2009; Schaum et al. 2018; West and Post 2016). Therefore, effects of warming on coexistence of two competing species might not only be caused by increasing phenological mismatch, but also via enhancing competition on basal resource (Fig. 1, mechanism ii).

Predators are generally assumed to have negative effects on prey abundance, and the strength of this effect can differ greatly among prey species (Karakoc et al. 2020; Paine 1966). Coexistence of competing prey species will be promoted when the predators are either specialists on the more competitive species, or generalists via density or frequency-dependent predation (Ishii and Shimada 2012; Karakoc et al. 2020; Saleem et al. 2012). However, studies also showed that predation can undermine coexistence if it is particularly strong (Bonsall and Hassell 1997; Chase et al. 2002), or if the rarer species is inefficient in resource consumption (Holt 1977). Eventually, species with the highest tolerance of predation will outcompete the others. Therefore, effects of predation on coexistence of competing species might be caused by the selective feeding by the predator (Fig. 1, mechanism iii).

Warming can affect the phenology of both predators and prey with implications for the effect of the predator on prey abundance (Zhang et al. 2018). Furthermore, warming will elevate the metabolic demands of predators which might strengthen the predator-prey interactions (Thakur et al. 2018; Thakur et al. 2017) and undermine prey coexistence (Thakur et al. 2017). Therefore, in addition to shifts in phenology and selective feeding, warming and predation might interactively enhance the pressure of a predator on its prey (Fig. 1, mechanism iv), with implications for prey coexistence.

Here we test the predictions that (1) Warming will alter the phenology and competition of two primary consumers; (2) Predation will reduce the abundance of the primary consumers; (3) Warming and predation will interactively increase the competition between primary consumers, reducing coexistence. To test these hypotheses, we used freshwater gastropods and their fish predators. Gastropods play key roles in aquatic ecosystems by contributing to nutrient cycling and water quality, particularly due to their role as algal grazers (Böhm et al. 2020; Strong et al. 2008). However, to our knowledge, no studies have investigated how warming and predation interact to alter their coexistence.

Materials And Methods

Study species

The targeted two gastropods *Bellamya aeruginosa* and *Radix swinhoi* are widespread in China, and commonly found to coexist in shallow aquatic ecosystems (Cai et al. 2018). *B. aeruginosa* is a branchiate gastropod (Gu et al. 2015), which feeds on sediment organic detritus, algae and bacteria (Liu et al. 1993). *B. aeruginosa* is a food resource for some fish (e.g. black carp, *Mylopharyngodon piceus*) and is also consumed by humans (Ma et al. 2010). The species is gonochoristic and ovoviviparous. The minimum temperature for the breeding of the snail is 16–18°C, and the optimal temperature is around 26°C (Chen and Song 1975). The reproductive cycle is about 6 months, and the snails can live for a few years. Adult females are gravid all year round and can release their newborn continuously in the breeding season (Ma et al. 2010).

R. swinhoi is a common pulmonated gastropod, which prefers habitat with macrophytes, and feeds on detritus, macrophytes, algae and even dead animal bodies (Li et al. 2005; Qi 1998; Zhi et al. 2020). It is hermaphrodite and allogamous, and it can breed multiple times a year (Qi 1998). *Radix* genus are generally cold-adapted gastropods (Pfenninger et al. 2006). Such as *R. balthica*, which prefers an optimum temperature of 16–20°C, and fails to reproduce over 24°C (Johansson et al. 2016; Johansson and Laurila 2017). The average life-span is about 30 weeks for *Radix* spp. (Lam 1994).

Experiment set-up

24 mesocosms (each of 2500 L in volume, diameter of 1.5 m, height of 1.4 m) at Huazhong Agricultural University, Wuhan, China, were used to simulate shallow lake ecosystems. Top layer sediment was collected from Lake Liangzi (N 30°11'3", E114°37'59"), which is a mesotrophic lake, with TN and TP of the water column in that area of about 0.43 mg L⁻¹ and 0.023 mg L⁻¹, respectively (Li et al. 2018). The location is rich of macrophytes, such as *Potamogeton crispus*, *Hydrilla verticillate*, *Ceratophyllum demersum* and *Trapa* sp. (Zhang et al. 2016). All mesocosms were filled with 10 cm of homogenized sediment on the bottom, and water were filled up to 1 m depth.

We used a fully-factorial design with two factors crossed - warming and predation - resulting in four treatments: Control (C), normal temperature with no fish; warming treatment (W), + 4.5°C higher than the temperature in the control; predation treatment (F), with a 60 g common carp (*Cyprinus carpio*); and

warming and predation treatment (WF). The temperature increase + 4.5°C was chosen to simulate the possible warming that could happen in this region at the end of this century (IPCC 2014), and temperature was manipulated automatically using two temperature sensors and a heating element controlled by a computer (Wang et al. 2020). Common carp is a typical omnivorous species which coexist with the two snails in water bodies in China, and the biomass of the fish in the mesocosms (equal to 340 kg ha⁻¹) is within the range found in the lakes at this region (Gao et al. 2014; He et al. 2019), and fish of this size could consume juvenile snails (Zhu et al. 2017). All fish were commercially obtained in a local aquarium shop. There were six replicates for each treatment, and all four treatments were randomly assigned to 24 mesocosms.

The experiment ran from February 2, 2015 to November 18, 2015. To indicate how the treatments affect the water quality during the experiment, water samples were collected once a week to analyze total nitrogen (TN), total phosphorus (TP), chlorophyll a (Chl. a), and turbidity. Methods for TN, TP and Chl. a analysis referred to the PRC National Standards. TN was first digested by alkaline potassium persulfate, and analyzed by UV spectrophotometry (UV-2800, Unico, China, GB 11894-89). TP was measured by ammonium molybdate spectrophotometric method (GB 11893-89). Chlorophyll-a was determined by filtering a certain amount of water on Whatman GF/C filters and spectrophotometric analysis after acetone extraction (HJ 897-2017). Turbidity was measured by a portable WGZ-2B turbidity meter (Xinrui, Shanghai, China). Periphyton Chl. a was measured by hanging a tile (10*10 cm²) in the middle of each mesocosm, weekly took out, brushed off the algae and extracted in acetone solution for 24 h, then analyzed by spectrophotometry. The biomass of the periphyton was expressed as the concentration of Chl. a per square centimeter area.

The density and biomass of snails were monitored once a week from March 14, 2015 to October 25, 2015. Snails were collected by vertically placing a tube (1.5 m in height, 4.5 cm in outside diameter, a total surface area of 0.1413 m²) attached to the wall of the mesocosm, the bottom of the tube was inserted into the sediment. The tube was taken out once a week, collected all snails, blotted dry, counted and weighted the snails to 0.0001g, and then released them back to the mesocosms.

Analyses

To analyze effects of warming, fish predation and their interaction on snail biomass, water quality, Chl. a concentrations in the water column and periphyton, multiple linear mixed effect models (LME) were deployed, with sampling date as a random factor. These dependent variables were log-transformed to increase the normality of the distribution. Normality and homoscedasticity of the dependent variables were assessed visually by plotting model residuals versus fitted values and in quantile-quantile plots of the model residuals. As the densities of both snails were count data, and as such a Poisson link function was applied to the generalized linear mixed effect model (GLMM). The effects of warming and predation were considered additive if models excluding their interaction term had lower AIC values. For the non-additive interactions, interaction effect sizes (*F*-values) were subtracted from the sum of the main effect sizes producing values representing the difference between additive and interactive effects, following

previous studies (Jackson et al. 2020; Lakeman-Fraser and Ewers 2014). If the value was positive, then the relationship was considered to be antagonistic (the effect of the drivers were reduced when acting interactively); if however, the value was negative, then the relationship was considered to be synergistic (the effect of the drivers were increased when acting interactively) (Table S1). All linear mixed models were performed using the lme4 package (Bates et al. 2015).

To assess the distribution patterns of the biomass and density of the snails over time, data from each mesocosm were fitted with a six parameters Weibull function using the cardidates package, which is designed for peak curve fitting (Rolinski et al. 2007). Not all peak curve fittings were trustable. Only the results of the biomass and density of *R. swinhoei* and some of *B. aeruginosa* in the control and warming treatments without fish present fitted well, as the fitted results for the rest did not match their trends well (Table S2). The heights and timing of peaks between control and warming treatments of *R. swinhoei* were compared using independent t-tests. Normality and homogeneity of variance were checked by shapiro test and *F*-test, respectively. To indicate the relative competition between the two snails in all treatments, normalized data (data were divided by the maximum value of each snail in each mesocosm to diminish their different scales) of the two snails were plotted together. All statistics were performed in R version 3.6.2 (Team 2019).

Results

Treatment manipulation

Daily averaged temperature was 4.25 ± 0.42 (n = 223, total number of days, mean $\pm$ sd) higher in the warmed mesocosms (Fig. 2a). Warming decreased the concentration of Chl. a in the water column, but increased concentration in periphyton samples (Table 1). Adding fish predators to the systems significantly increased turbidity, and concentrations of Chl. a in the water column and periphyton (Table 1 and Fig. 2b,c,d). In the warming treatments, adding fish predators increased the turbidity more than warming alone. Warming and fish predation also interactively affected the Chl. a concentration in the water column (Table 1 and Fig. 2c). Data of TN and TP can be found in Fig. S1. No significant increase of biomass of fish was found at the end of the experiment.

Snail response

In all treatments, snail biomass was dominated by *B. aeruginosa*. Snail density was dominated by *R. swinhoei*, but only when no fish were present (Fig. 3). Both warming and predation significantly decreased the biomass and density of the two snails, and the effects of predation was stronger than that of warming (Table 1 and Fig. 3). The combined effects of warming and predation were additive for the biomass of *B. aeruginosa* (AIC value was smaller in the model without interactive factor, Table S1), while the effects were antagonistic for density of *B. aeruginosa* ($\Delta F = 20.4$). The effects of warming were amplified under fish predation on both biomass ($\Delta F = -4.0$) and density ($\Delta F = -220.4$) of *R. swinhoei* (Table S1).

The average timing of peak density in *R. swinhoei* was 21.5 days earlier in the warming treatment (without fish) than in the control (Welch t-test, Table S3). However, the peak densities of *R. swinhoei* were not significantly different between warming treatment and control. The peak biomass and average time of peak biomass of *R. swinhoei* did not differ significantly under control and warming treatment without fish (Table S3). The time of peak biomass and density of *B. aeruginosa* varied largely within treatments, and the variations increased with warming (without fish) compared to control, some were advanced (n = 4) and one was delayed (n = 1) (Table S2 and Fig. S2). No clear peaks of the two snails could be detected in the treatments with fish present.

The overlaps between the two snails shifted with warming and predation. Peaks of biomass and density of *B. aeruginosa* were found reduced and shifted under warming without fish present, and clear pits were observed in biomass and density of *B. aeruginosa* when these peaks reached for *R. swinhoei* in the warming treatment without fish (Fig. S3). In the ambient treatment with fish present, peaks of biomass and density of *B. aeruginosa* were advanced, while the biomass and density of *R. swinhoei* increased over time and the highest values occurred at the end of the experiment. In the warming treatment with fish present, the biomass and density of *B. aeruginosa* decreased over time, and the highest values occurred at the beginning of the experiment, while the biomass and density of *R. swinhoei* were always low and increased gradually (Fig. S3). These imply that both snails were suppressed more under warming with fish present, particularly for *R. swinhoei*.

Discussion

Our results show that warming and fish predation interact to alter the phenology and demography of aquatic snails. The biomass and density of both snails declined with warming and adult *B. aeruginosa* dominated in the fish predation treatment. Warming and fish predation combined in an additive manner to decrease the biomass of *B. aeruginosa*, while its density declined less than expected (i. e. there was an antagonistic interaction between the stressors). Warming and fish predation interacted to amplify their independent effects on the biomass and density of *R. swinhoei*, causing a decline larger than expected by an additive response (i. e. a synergistic interaction). Both warming and predation induced higher periphyton biomass due to a trophic cascade. We discuss the underlying mechanisms and implications for freshwater ecosystems below.

Warming effects on coexistence of snails

In our study, warming significantly advanced the peak of reproduction of *R. swinhoei* by 21.5 days. Past studies have shown that warming advances the phenology of species across different trophic levels including plants (Zhang et al. 2016), algae (Hansson et al. 2013), zooplankton (Velthuis et al. 2017) and fish (Tao et al. 2018), with the phenology of primary consumers generally advanced more than other trophic levels (Thackeray et al. 2016). In our study, the advanced days of reproduction for *R. swinhoei* was almost the same amount of days earlier in warming treatments than in the ambient when temperature reached > 24°C. Species in this genus (*Radix spp.*) are normally cold-adapted species

(Pfenninger et al. 2006) and, therefore, when temperature reached $> 24^{\circ}\text{C}$, the snails fail to reproduce (Johansson et al. 2016; Johansson and Laurila 2017). In contrast, no consistent peaks of biomass and density could be detected for *B. aeruginosa*, which could be attributed to the different life-history traits of the snail. *B. aeruginosa* has a much higher upper-limited thermal tolerance, as its optimal reproduction temperature is $\sim 26^{\circ}\text{C}$ (Chen and Song 1975), and the snail has a life span which can last for a few years. Furthermore, the female can be gravid all year round and release offspring continuously in the breeding season (Ma et al. 2010). Field investigations have also found multiple different peaks of abundance and biomass for *B. aeruginosa* throughout the year (Chen 1987; Gong et al. 2009; Yan et al. 2000). However, the time of peak biomass and density of *B. aeruginosa* did show differences between the ambient and warming treatment without fish present, which indicates that warming still altered the phenology of the snail, while the effect was inconsistent, could either be advanced or delayed. This might be because the effects of warming on the snail were different among ages.

Warming decreased the biomass and density of both snails, and there are two key reasons which can explain these changes linked to phenology and feeding rates. Firstly, warming altered the phenology of both snails. *R. swinhoei* is hermaphrodite and its reproductive cycle can be completed in eight weeks, whereas *B. aeruginosa* is gonochoristic and ovoviviparous, and its reproductive cycle is about 6 months (Ma et al. 2010). During the growing season of *R. swinhoei*, this species can reproduce faster and dominate in abundance, while the *B. aeruginosa* will respond slower to rising temperatures from spring to summer. In the warming treatments, the advancement of reproduction by *R. swinhoei* strongly suppress the population of *B. aeruginosa*, as clear pits were observed in biomass and density of *B. aeruginosa* when these peaks reached for *R. swinhoei* in the warming treatment (Fig. S3). This might be because that *R. swinhoei* depleted algal food resources in the growing season, thus reducing fecundity of *B. aeruginosa*. In our study, the standing biomasses of periphyton were very low in both ambient and warming treatment in the early growing season. These indicate that a strong grazing pressure on periphyton by the snails in the early growing season. Furthermore, the phenology of periphyton does not advance at the same rate as consumers with warming (Thackeray et al. 2016) and, therefore, there are less resources available when the snails reproduce in a warmer world. The competition between the two snails was strong, and *R. swinhoei* was more competitive in the growing season. In addition, top-down pressure might be enhanced with warming (Schaum et al. 2018), which means that an even stronger competition could happen between the two snails due to limited food source. Therefore, snail density and biomass both decreased due to warming.

Predation effects on coexistence of snails

As expected, the biomass and density of the two snails were suppressed in the presence of fish (Karakoc et al. 2020; Paine 1966). The predation effects were particularly strong on *R. swinhoei* and the juveniles of both snails. This is because crucian carp can only prey on snails smaller than their jaw gape, hence, they substantially eliminated the juveniles of both snails. Furthermore, the adult individual biomass was larger in *B. aeruginosa* (can reach 5.77 g) than in *R. swinhoei* (hardly larger than 1.5 g), and shell toughness was much higher in *B. aeruginosa* than in *Radix spp.* snail (Zhu et al. 2013; Zhu et al. 2017).

Therefore, we observed adult *B. aeruginosa* dominated in the predation treatment, particularly in the beginning, since *R. swinhoi* was preferentially consumed by the fish. These indicate that predation increased the relative competence of *B. aeruginosa* over *R. swinhoi* at the early time and the competence shifted over time.

The presence of fish strongly disturbed the water promoting the growth of periphyton. We expected this higher turbidity and periphyton biomass to partly alleviate the predation effect from the fish, due to both declining visibility and increase food resources for the snail. However, in our study, the density of fish added to the system was high (Gao et al. 2014), and no such effects were observed. Under a strong predation pressure, *B. aeruginosa* might exclude *R. swinhoi* in the ecosystem eventually by undermining the balance of coexistence in the competing species (Bonsall and Hassell 1997; Chase et al. 2002).

Interactive effects of warming and predation on snails

Warming and predation combined additively to decrease the biomass of *B. aeruginosa*, and antagonistically to decrease its density. This suggests warming and predation combined to mitigate one another's independent effects on this species. This might be because warming increased the availability of algal resources for the snails with fish presence, which partly alleviate the predation effect from the fish. In contrast, there was a synergistic interaction between warming and predation on *R. swinhoi*, resulting in large declines in its biomass and density. Top-down control by predators on prey is enhanced by warming (Hansson et al. 2013). Here, the crucian carp exerted stronger pressure on *R. swinhoi*, the preferred food (Zhu et al. 2017) under warming. This caused a significant amplified interaction of warming and predation on the growth and reproduction of *R. swinhoi*. Warming has also shown to affect attack rate, handling time and predation success (Twardochleb et al. 2020). However, in our study, the prey are rather slow-moving species, the impacts of warming on the predation was mainly determined by the increased feeding rate, and the prey are unlikely to develop strongly avoidant mechanisms against predation in one or two generations. In a longer period, continuous warming and strong predation might eventually undermine the coexist of the two snail species, excluding *R. swinhoi*.

Implications for aquatic ecosystems

In our study, warming and predation interactively enhance the competition between the two snails, decreasing the biomass and density of both snails, resulting in higher growth of periphyton. The trophic cascading effects could have substantial impacts on aquatic food webs. With the decrease of gastropods, fish population might decrease over time (Nagelkerken and Connell 2015), but periphyton growth increase, resulting in bottom heavy trophic pyramid. This might hinder the nutrient cycle and energy transfer in the aquatic ecosystem (Nagelkerken et al. 2020). Furthermore, continuous warming and strong predation might undermine the coexistence of the two snails, eventually causing local extinction of the less dominate species (Fig. 4). The loss of key primary consumer not only decreases biodiversity, but might also weaken the stability of aquatic food webs (Ives and Cardinale 2004; Nagelkerken et al. 2020). Particularly in shallow lakes with strong anthropogenic activities, as eutrophication, chemical pollution and habitat destruction are common in these areas (Birk et al. 2020;

Steffen et al. 2015). These might interactively alter the shallow aquatic ecosystem from a health state to a nuisance state, leading to loss in ecosystem functions and services (Scheffer et al. 2001). Future studies should investigate more on how warming could affect species coexistence in other model systems in longer time, and how these will further alter food web structures in ecosystems.

Table 1

Effects of warming and predation on the measured response variables and snail biomass and density. Water turbidity, Chl. a concentrations in the water column and periphyton, and snail biomass are analyzed by linear mixed effect models, and snail densities are analyzed by generalized linear mixed effects models with a Poisson link function. Bold number indicates a significant level of < 0.05.

	Parameters	Factor	Estimate	se	t/z	p
Measured response variables	log(Turbidity + 1)	Intercept	1.50	0.11	13.47	< 0.0001
		Warming	-0.08	0.10	-0.76	0.4455
		Fish	1.19	0.10	11.82	< 0.0001
		Warming*Fish	1.09	0.14	7.63	< 0.0001
	log(Chl. a + 1)	Intercept	1.75	0.05	33.97	< 0.0001
		Warming	-0.18	0.07	-2.78	0.0054
		Fish	0.61	0.07	9.22	< 0.0001
		Warming*Fish	0.50	0.09	5.30	< 0.0001
	log(Periphyton + 1)	Intercept	1.24	0.07	18.35	< 0.0001
		Warming	0.64	0.08	8.45	< 0.0001
		Fish	0.83	0.08	11.04	< 0.0001
		Warming*Fish	0.01	0.11	0.05	0.9582
B. aeruginosa	Log(Biomass + 0.01)	Intercept	1.56	0.26	6.00	< 0.0001
		Warming	-1.09	0.34	-3.20	0.0014
		Fish	-1.83	0.34	-5.35	< 0.0001
		Warming*Fish	-0.02	0.48	-0.05	0.9625
	Density	Intercept	1.82	0.08	22.01	< 0.0001
		Warming	-0.29	0.04	-6.66	< 0.0001

Parameters		Factor	Estimate	se	t/z	p
R. swinhoei	Log(Biomass + 0.01)	Fish	-1.38	0.06	-21.54	< 0.0001
		Warming*Fish	-0.22	0.10	-2.14	0.0327
		Intercept	-0.42	0.26	-1.60	0.1095
		Warming	-0.79	0.23	-3.35	0.0008
	Density	Fish	-2.79	0.23	-11.90	< 0.0001
		Warming*Fish	0.60	0.33	1.80	0.0714
		Intercept	2.74	0.33	8.23	< 0.0001
		Warming	-0.54	0.02	-27.39	< 0.0001
Density	Fish	-3.02	0.06	-54.61	< 0.0001	
	Warming*Fish	0.89	0.07	12.22	< 0.0001	

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Figures

Figure 1

Possible mechanisms of warming and predation and their interactive effects on the coexistence of two competing species. (i) Shifting in phenology; (ii) increasing top-down control on resource; (iii) preferred feeding on one prey species; and (iv) enhancing top-down control on both prey. Solid arrow indicates energy transfer pathway, dashed arrow indicates competition, and red and blue arrows indicate an enhanced interaction and an unaffected interaction, respectively.

Figure 2

Daily averaged temperature, water turbidity, and Chl. a concentrations in the water column and periphyton changed over time in different treatments. In panel a, the horizontal dotted and dashed lines indicate temperature of 16 $^{\circ}\text{C}$ and 24 $^{\circ}\text{C}$, respectively. When the averaged temperature started to go above 24 $^{\circ}\text{C}$, the days were 113 and 134 for the warming and ambient treatments, and these are indicated by vertical red and blue lines, respectively. Panel b, c and d share the same legend. Vertical bars are standard errors. C for control, W for warming, F for predation and WF for warming and predation.

Figure 3

Biomass and density of the two snails changed over time in different treatments. Biomass (a) and density (b) of *B. aeruginosa*, and biomass (c) and density (d) of *R. swinhoei*. The curves were fitted from the loess model in R package ggplot2. Vertical bars are standard errors. The vertical lines in panel d indicate the time of the peak density, which extracted from the fitted Weibull-functions, and the time of peak for the warming treatment without fish was 21 days earlier than the control. C for control, W for warming, F for predation and WF for warming and predation. Please note that the y-axis is on different scales for each species.

Figure 4

Summary diagram of warming and predation stress on the coexistence of the two gastropods and resulting impacts on periphyton biomass. Over the longer term, *R. swinhoi* might be excluded from the coexistence and the food web structure will be simplified.

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