

## Research

### Ectothermic omnivores increase herbivory in response to rising temperature

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Higher temperatures as a consequence of global climate change may considerably alter trophic interactions. Ectothermic herbivores and carnivores generally ingest more food with rising temperature as their metabolic rates increase with rising temperature. However, omnivorous ectotherms may respond in two ways: quantitatively by consuming more food and qualitatively by altering their degree of herbivory or carnivory through a diet shift. We hypothesize that rising temperature will increase herbivory of ectothermic omnivores as herbivory increases towards the equator. We tested the hypothesis in a freshwater model system in which ectothermic omnivores are prevalent, by applying two approaches, a temperature manipulation experiment and a literature study. We performed feeding trials with a juvenile aquatic ectothermic omnivore (pond snail *Lymnaea stagnalis*) at different temperatures ranging from 12 to 27°C, supplying them with both animal food and plant material, and directly quantified their consumption rates over time. The results showed that snails cultured at high temperatures (> 21°C) increased the proportion of plant material in their diets after 17 days, which supports our hypothesis. In the literature survey, we found that rising temperature increased herbivory in multiple aquatic animal taxa, including zooplankton, amphibians, crayfish, fish and snails. This suggests that aquatic ectothermic omnivores might commonly increase herbivory with rising temperature. The mechanisms underlying this temperature-induced diet shift are not sufficiently explained by current theories related to the physiology, metabolism and stoichiometry of omnivores. We propose to incorporate the animals' ontogenetic development in the temperature metabolic stoichiometry hypothesis as a complementary explanation for the diet shift, namely that the diet shift could be due to faster development of the ectotherms and an earlier ontogenetic diet shift at higher temperatures. We conclude that future global warming will most likely alter food webs by increasing the top-down control of aquatic herbivores and omnivores on primary producers.

Keywords: climate change, diet shift, food selection, poikilotherm, pond snail, temperature rise, trophic interaction



## Introduction

Due to anthropogenic activities, our planet is undergoing rapid climate change, which includes both a temperature rise and an increase in the occurrence of climate extremes (IPCC 2014). Temperature, as the fundamental abiotic factor underlying climate change, can directly influence the metabolism of organisms (Gillooly et al. 2001, Brown et al. 2004), thereby influencing trophic interactions, food web structures and the functioning of ecosystems (Traill et al. 2010, Hansson et al. 2013, Cross et al. 2015, Schaum et al. 2018, Zhang et al. 2018a). For ectotherms, their metabolic rates increase sharply with rising temperature (Brown et al. 2004), resulting in increased food consumption. In the case of herbivores and carnivores, this implies enhanced feeding pressure on lower trophic levels at higher temperatures. However, the response of omnivorous ectotherms to rising temperatures is less straightforward, as they may respond in two ways: 1) quantitatively by consuming more food and 2) qualitatively by altering their degree of herbivory or carnivory through a diet shift.

Across latitudinal gradients, there is a prevalence of herbivory towards the equator in fish communities (Floeter et al. 2005, Jeppesen et al. 2010, Moss 2010, Behrens and Lafferty 2012, González-Bergonzoni et al. 2012). Many explanations for this latitudinal trend have been proposed, including evolutionary constraints, food availability and food quality, but this also includes the hypothesis that temperature is the key factor underlying this latitudinal trend (Floeter et al. 2005, González-Bergonzoni et al. 2012). If herbivory increases towards lower latitudes due to higher temperatures at the equator, this suggests that omnivorous animals may also shift towards a more plant-based diet at higher temperatures. Hence, future global warming could have more impacts on ecosystems than anticipated, by altering the trophic level of animals and thereby changing the abundance or composition of primary producers. This implies that there is an urgent need to test whether an increase in temperature would change the diet selection of omnivores.

### Possible mechanisms causing temperature induced diet shifts

There are several possible mechanisms that may underlie temperature-induced diet shifts in omnivores (Fig. 1). First, the temperature physiological constraint hypothesis (TPCH), which was initially developed for fish, poses that omnivores cannot meet their energetic demands by only consuming plant materials at low temperatures (Gaines and Lubchenco 1982, Floeter et al. 2005). Although both metabolic rates and feeding rates generally decrease with decreasing temperatures, feeding rates decrease faster than metabolic rates as temperature decreases (Floeter et al. 2005). Furthermore, digesting cellulose in plant material requires the activity of microorganisms in the digestive system, which grow best above certain temperatures (Vejříková et al. 2016). Compared to plant material, animal food items are easier to digest at low

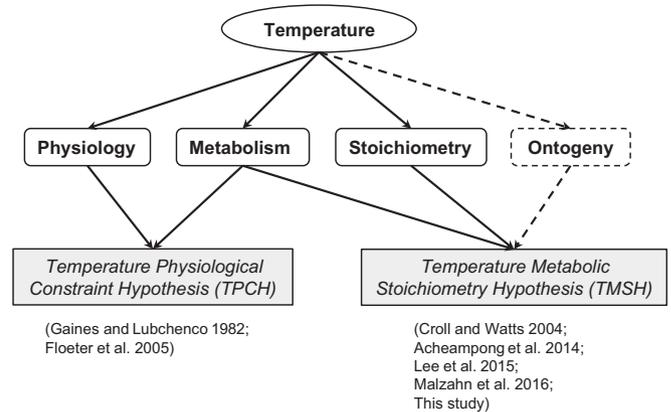


Figure 1. Schematic graph of possible mechanisms for increased herbivory by aquatic omnivores with rising temperature. Temperature influences different aspects of the omnivores and the hypotheses are based on these effects. The dashed lines indicate the possible mechanism of ontogeny that we propose to include as an explanatory mechanism based on the results from our study.

temperatures and higher in nutrient content, hence ectothermic omnivores ingest more animal food at low temperatures (Behrens and Lafferty 2007). However, there are also large herbivorous fish in cold regions which can digest plant material, as they have long digestive tracts to increase the food retention time needed for digestion (Targett and Arnold 1998, Clements et al. 2009). Additionally, the abundance of herbivorous fish populations was found to be higher at high latitudes than at low latitudes in the southern hemisphere, which does not support the TPCH (Trip et al. 2014). Therefore, the TPCH alone might not be sufficient to explain why the omnivores increase the degree of herbivory with increasing temperature.

An alternative explanation might be achieved under the framework of ecological stoichiometry theory (Sterner and Elser 2002) and metabolic ecology (Brown et al. 2004). The temperature metabolic stoichiometry hypothesis (TMSH), predicts that ectotherms need to consume food with a higher carbohydrate:protein (or carbon (C):nitrogen (N)) ratio at higher temperatures (Croll and Watts 2004, Acheampong et al. 2014, Lee et al. 2015, Malzahn et al. 2016). As temperature increases, ectotherm animals need to obtain more energy to sustain their increased metabolism, resulting in an increased ingestion rate. However, the respiration rate (catabolic) of animals increases faster than their growth rate (anabolic) as temperature increases (Karl and Fischer 2008, Forster et al. 2011). Therefore, ectothermic animals need to consume relatively more carbohydrates to sustain their increased metabolism. As plants generally have a higher C:N ratio than animals (Zhang et al. 2018b), this could explain why omnivorous ectotherms include more plant material in their diet at higher temperatures, if part of the C is available as carbohydrates. Plant material can be rich in digestible carbohydrates (e.g. sugars and starches), as found in aquatic plants (Chou et al. 2019) and algae (John et al. 2011). However, rising temperatures can also increase the

preference for protein (N rich) such as shown in grasshoppers (Schmitz et al. 2016), and the preference for carbohydrates and protein was inconsistent with rising temperatures in mealworm beetles (Rho and Lee 2017). Furthermore, model simulation showed that the requirement of zooplankton of a certain food C:N ratio would not change with increasing temperature if the increased amount of food intake is taken into consideration (Anderson et al. 2017). Together, these observations suggest that more work is needed before we can judge the generality of the TMSH hypothesis.

To date, no study has tested a potential diet shift in ectotherm omnivores at different temperatures over time, and when the shifts happen is also not clear. Here, we applied two approaches to test whether ectothermic omnivores would increase the proportion of plant material in their diet with rising temperatures. 1) We performed an experiment with juveniles of a widespread ectotherm, the pond snail *Lymnaea stagnalis*, to test its diet selection over time at different temperatures. *Lymnaea stagnalis* is a generalist omnivore, which can feed on a wide variety of food, including periphytic algae and macrophytes, as well as carrion, e.g. dead crayfish, insects, frog tadpoles, fish and even snails (Bovbjerg 1968, Brönmark 1989, Elger and Barrat-Segretain 2004, Zhang et al. 2019). Generally, the snail reaches adulthood when its shell length is above 2.4 cm, and the snails can reach 3.0 cm in eight weeks from hatching under favourable conditions (Van der Schalie and Berry 1973, Elger and Barrat-Segretain 2002, Koene et al. 2006). The snails can survive for a few years in nature, and live in a range of temperatures from 6 to 30°C, with an optimum for growth and reproduction between 20 and 25°C (Van der Schalie and Berry 1973, Zhang et al. 2018b). 2) We provided an overview of previously published effects of temperature on the diets of omnivores, integrating our own data. We tested the hypothesis in a freshwater model system as most aquatic animals are ectotherms (Isaak and Rieman 2013), and omnivorous feeding modes are prevalent in aquatic ecosystems, where many animals can consume both plant material and animal food (Wootton 2017).

## Material and methods

### Agar-based food preparation

To test the effects of temperature on diet selection, we first created agar-based foods using two common food sources, plant food *Elodea nuttallii* and animal food Chironomidae larvae. The two types of food are very common in the habitat

where the pond snails live. The advantage of agar-based food is that we could remove the structural differences and focus on the nutritional differences of the food types. This method has been applied in many other experiments to test the feeding behaviour of aquatic animals (Kampfraath et al. 2012, Crenier et al. 2017). The reason to choose *E. nuttallii* as the plant food source in the experiment was that it is a cosmopolitan aquatic plant and also a palatable plant for aquatic animals, including the pond snail *L. stagnalis* (Elger and Barrat-Segretain 2004, Grutters et al. 2017), fish (Dorenbosch and Bakker 2011) and waterfowl (Bakker and Nolet 2014). *Elodea nuttallii* was collected in a pond on the terrain of NIOO-KNAW, Wageningen, the Netherlands (51°59'12.7"N, 5°40'15.4"E). Plants were thoroughly cleaned and freeze-dried. Chironomidae larvae were selected as the animal food source, as it is a common animal food type eaten by many aquatic animals (Armitage 1995). Freeze-dried Chironomidae larvae were commercially obtained. To facilitate stoichiometric interpretations of diet choice by the animals, the C and N content were measured in samples from dried plant material and animal food (Table 1) using an auto elemental analyzer.

Before food was offered to individual animals in choice experiments, we standardized the texture and concentration of the food by grinding the food to powder through a 0.5 mm sieve and subsequently mixing the powder into agar solutions (P1001). Ratios of food:agar were determined by pre-trials (Table 1). The water content in agar-based food was comparable to the actual food, as the water content all around 90% (Armitage 1995, Zhang et al. 2019). The agar-based food would partly dissolve in the water, and the animal material dissolved more in the water than the plant material as appeared from our tests (Supplementary material Appendix 1 Table A1). In order to offer similar concentrations of plant and animal material of agar-based food to the snail after dissolving, we mixed more animal material into the agar as calculated from pre-trials (Table 1). The agar food was made according to the following procedure (Crenier et al. 2017): cooking the agar in demineralized water in a microwave until it completely dissolved; stirring the solution until it cooled down to 55°C; adding a predetermined amount of ground plant or animal material and stirring until well-mixed and pouring the mixture into a polyethylene mould with 100 holes with a diameter of 7 mm and height of 5 mm. The mould was constructed of two polyethylene boards and four clamps, holes were drilled on the top one and the bottom one was a flat substrate, the agar-filled mould was left at 4°C for

Table 1. Original nutrient concentration and stoichiometry of the food and the agar food composition used in the experiment. All data are means  $\pm$  SD, n=3. Weights are dry weight. Significant differences between the plant and animal food (independent t-tests) are indicated by different letters for each component.

Food type	Original food nutrients			Agar food composition		
	C (mgg <sup>-1</sup> )	N (mgg <sup>-1</sup> )	C:N (gg <sup>-1</sup> )	Agar (g)	Demineralized water (ml)	Food materials (g)
Plant	334.9 $\pm$ 2.1 <sup>a</sup>	32.5 $\pm$ 1.4 <sup>a</sup>	10.3 $\pm$ 0.45 <sup>a</sup>	1	50	2.5
Animal	355.6 $\pm$ 6.7 <sup>b</sup>	76.3 $\pm$ 1.3 <sup>b</sup>	4.66 $\pm$ 0.03 <sup>b</sup>	1	50	4

2 h. The agar pellets were collected from the mould and stored at 4°C until use (maximum preservation of three days). The plant and animal agar food could be visually distinguished, because the plant food was dark green and animal food was brown (Supplementary material Appendix 1 Fig. A1).

### Experimental trials

Adult pond snails were originally obtained from another pond at the terrain of NIOO-KNAW (51°59'17.5"N, 5°40'28.5"E) and kept in the lab, where they reproduced. Egg clusters were hatched, and reared in plastic buckets at 20°C, which is a suitable temperature for the snails to grow (Van der Schalie and Berry 1973). The buckets were filled with tap water and constantly aerated, and exposed to a day:night cycle of 16:8 h. Hatched snails were fed ad libitum with commercially obtained lettuce and fish food, following established successful rearing methods (Elger and Barrat-Segretain 2002, Grutters et al. 2017, Zhang et al. 2019). After culturing for one month, 48 (6 temperatures × 8 replicates) juvenile snails with a shell length of  $1.21 \pm 0.07$  cm (mean ± SD) were selected for the experiment. Each snail was put in a plastic beaker (top diameter 12.5 cm, bottom diameter 11 cm and height 11 cm), filled with 500 ml temperature-acclimated tap water and covered with mesh to prevent the snails from escaping. Four beakers were set in one styrofoam platform, and placed in one aquarium (90 × 50 × 50 cm, l × w × h) in a 30 cm layer of water. The aquaria functioned as a water bath set at six temperatures: 12, 15, 18, 21, 24 and 27°C. We varied the temperature between 12 and 27°C, where at the minimum temperature the snail would still be feeding enough to yield a measurable consumption rate and at the maximum temperature would still survive (Van der Schalie and Berry 1973). Every two aquaria were controlled at the same temperature, and the temperatures were randomly assigned to 12 aquaria in one room. The light intensity on the water surface was  $10.35 \pm 0.28 \mu\text{mol m}^{-2} \text{s}^{-1}$  (mean ± SD, n = 5), with a day:night cycle of 12:12 h. These low light levels were within the normal range of where the snails live.

During the experimental trials, snails were offered both plant-based and animal-based agar pellet food ad libitum. Leftover food was checked every day for each snail to make sure they had enough of both types of food for the next day; if not, new agar food pellets were added. Every three days, water was replaced and the bucket was cleaned for each snail, meanwhile, leftover food was retrieved, put in a pre-weighed aluminium cup, dried in the oven at 60°C for 48 h and weighed to quantify final food dry weight. New food pellets of both types of plant and animal food were supplied to each snail, and quantities were increased if necessary, to provide ad libitum food of both food types. The number of pellets offered to the snails varied from one pellet of each type at the start of the experiment to maximum of seven plant pellets and 10 animal pellets in the highest temperature treatment at the end of the experiment. The plant to animal food ratios offered to the snails varied between 1:1 and 1:4. However, these relative differences in the amount of food for each food

type offered to the snails did not affect their feeding preferences, as the snails at the higher temperatures started to select more plant food over time, despite the fact that relatively more animal food was offered. *Lymnaea stagnalis* has a strong sense for food by perception of volatile organic compounds released by the food (Moelzner and Fink 2014) and therefore would not have problems to distinguish between the food types or to find the preferred food. The snails are known to go strongly for the food they prefer, even though they encounter more of the unpreferred food (Zhang et al. 2018b, c). Agar food can lose some weight over time as part of it may dissolve in the water. Therefore, we performed dissolving trials at different temperatures and initial dry weight of an agar food pellet in the snail feeding trial was estimated based on these dissolving trials (Supplementary material Appendix 1 Table A1). The food consumption rate was expressed as how much food was consumed by each snail per day: (food initial dry weight – food final dry weight)/days. The experiment lasted for 24 days from 20 October to 12 November 2017 and snail wet weight and shell length were measured at the start and end of the experiment. Snail relative growth rate was expressed as:  $[\ln(\text{final snail weight}) - \ln(\text{initial snail weight})]/\text{days}$ .

### Data analysis

General linear mixed-effects models were employed to analyse the effects of temperature on plant food consumption rates, animal food consumption rates and the plant:animal food consumption ratio of the omnivore over time. Both temperature (ranging from 12 to 27°C) and time (in days) were included in the models as continuous explanatory variables. Aquarium and species identification number were included as random factors to account for the dependency structure in our experimental design and for the repeated measurements, respectively. 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. All the dependent variables were log-transformed to improve their normality before performing the analysis.

To measure food consumption in dry mass, we converted wet weights into dry weights, which introduced slight measurement errors, resulting in a few negative values (n = 6 for plant consumption rates and n = 10 for animal consumption rates, these mainly happened in the first few days of the experiment). We replaced those negative values by a small positive value of 0.1 mg, as negative consumption rates are ecologically meaningless, whereas replacing them by 0 mg would not allow us to calculate the ratio of plant:animal food consumed when the denominator was zero. To test whether this affected the results, we also tried to standardize those negative values to 0 mg, or removed them or retained them all, none of these methods changed the qualitative outcome of the data analysis and the statistical significance. We chose to standardize all negative consumption rate values to 0.1 mg, as herewith we retained all data and all data are ecologically

meaningful, following previous analyses of these types of feeding trials (Grutters et al. 2017). Diet selection was indicated by the ratio of plant food consumption rate to animal food consumption rate. All statistics were performed in R ver. 3.4.3 (<www.r-project.org>) and for the mixed-effect models we used package nlme (Pinheiro et al. 2017).

## Literature study

In addition to our experiment we also surveyed the available experimental evidence for effects of temperature on the diets of omnivorous ectothermic animals in the literature. We therefore used the following search terms in ISI: Web of Science: 'temperature' OR 'warm\*' OR 'heat' in the title, 'omnivor\*' and 'diet' OR 'food' in the topic, and checked for cross-references in the obtained literature. This resulted in 64 publications, of which 10 publications presented suitable experimental data on how the diet of omnivorous ectotherms responded to changing temperatures. This resulted in a database with 14 cases, covering 5 taxa and 10 species of aquatic animals which included our own experiment.

## Results

### Snail experiment

The animal food had a higher N content and a lower C:N ratio than the plant food used in the experiment (Table 1). Pond snails increased their plant food consumption rates in response to rising temperature, and when temperatures were  $\geq 15^{\circ}\text{C}$ , pond snails increased plant consumption rates over time (Fig. 2a, Table 2). Animal food consumption rates by pond snails increased with temperature rise and increased over time at all temperatures (Fig. 2b, Table 2). Temperature effects on the plant:animal consumption ratios emerged after 17 days; snails significantly increased plant:animal consumption ratios afterwards when temperatures were above  $21^{\circ}\text{C}$  (Fig. 2c, Table 2). The average plant:animal food consumption ratio over the entire experiment was  $0.15 \pm 0.14$  (mean  $\pm$  SD,  $n=327$ ). Both snail final shell length and relative growth rate significantly increased with temperature and levelled off from  $24^{\circ}\text{C}$  (Fig. 3). At the end of the experiment, snails had 1.6 times longer shells and 2.2 times faster relative growth rates at  $24^{\circ}\text{C}$  than at  $12^{\circ}\text{C}$ . No indication was found that the snails were suffering of dietary limitations in the experiment.

### Literature survey

No study using a terrestrial model system to test effects of temperature on omnivorous diet selection was found. Rising temperature increased the degree of herbivory by aquatic omnivores in 12 of the 14 cases in our acquired dataset, which includes taxa in zooplankton, amphibians, crayfish, fish and aquatic snails (Table 3). The two approaches to study potential effects of temperature on omnivore diets were

temperature manipulation experiments (11 cases) and seasonal comparison (3 cases). Differences between the lowest and highest temperature tested in each case ranged from 4 to  $20^{\circ}\text{C}$ . Among the 11 cases that manipulated temperature, the duration of the experiment ranged from 24 h to 2 months. Six cases focused on fish, and all found temperature effects on diet selection, such that rising temperatures increased the proportion of plant material in the fish diets.

## Discussion

The pond snails increased their consumption rates and degree of herbivory with rising temperature in our study, which confirms that the omnivore quantitatively increased its food consumption rates and qualitatively shifted to more herbivory with rising temperature. Furthermore, through the combination with a literature study, we found that several aquatic omnivores increased their degree of herbivory when water temperatures increased, and only two experimental cases out of 14 did not find a diet shift with rising temperatures. In the following sections, we will discuss possible reasons for the absence of a diet-shift in these studies, and discuss the implications of qualitative changes in omnivore diets for aquatic food webs, as well as provide perspectives for future studies on this timely topic.

### Increased consumption and herbivory with rising temperature

With rising temperature, the consumption rate of snails in our experiment increased, which is consistent with previous studies (González-Bergonzoni et al. 2016, Zhang et al. 2018b). For ectotherms, the metabolic and consumption rates of organisms increase as temperature increases (Gillooly et al. 2001, Brown et al. 2004), until an optimum temperature is reached, after which then biological rates sharply decline (Sinclair et al. 2016, Rohr et al. 2018). The pond snail used in our experiment has an optimum temperature for growth and reproduction between  $20^{\circ}\text{C}$  and  $25^{\circ}\text{C}$  (Van der Schalie and Berry 1973, Zhang et al. 2018b), the maximum temperature in our experiment. Similar to other studies, we observed an increase of consumption rate of snails with rising temperatures, and a stronger plant–consumer interaction with rising temperature.

Through the combination of a controlled experiment and a literature study, we found that studies supporting the hypothesis that rising temperature increases herbivory of aquatic omnivores covered five aquatic taxa, including zooplankton (Boersma et al. 2016), tadpoles (Carreira et al. 2016), crayfish (Carreira et al. 2017), aquatic snails (this study) and fish (Prejs 1984, Behrens and Lafferty 2007, Guinan Jr et al. 2015, Emde et al. 2016, González-Bergonzoni et al. 2016, Vejříková et al. 2016). It is important to note that even though the authors observed diet shifts in the three seasonal comparison studies, there still could be other reasons accounting for the diet shift, such as changes in food abundance and food

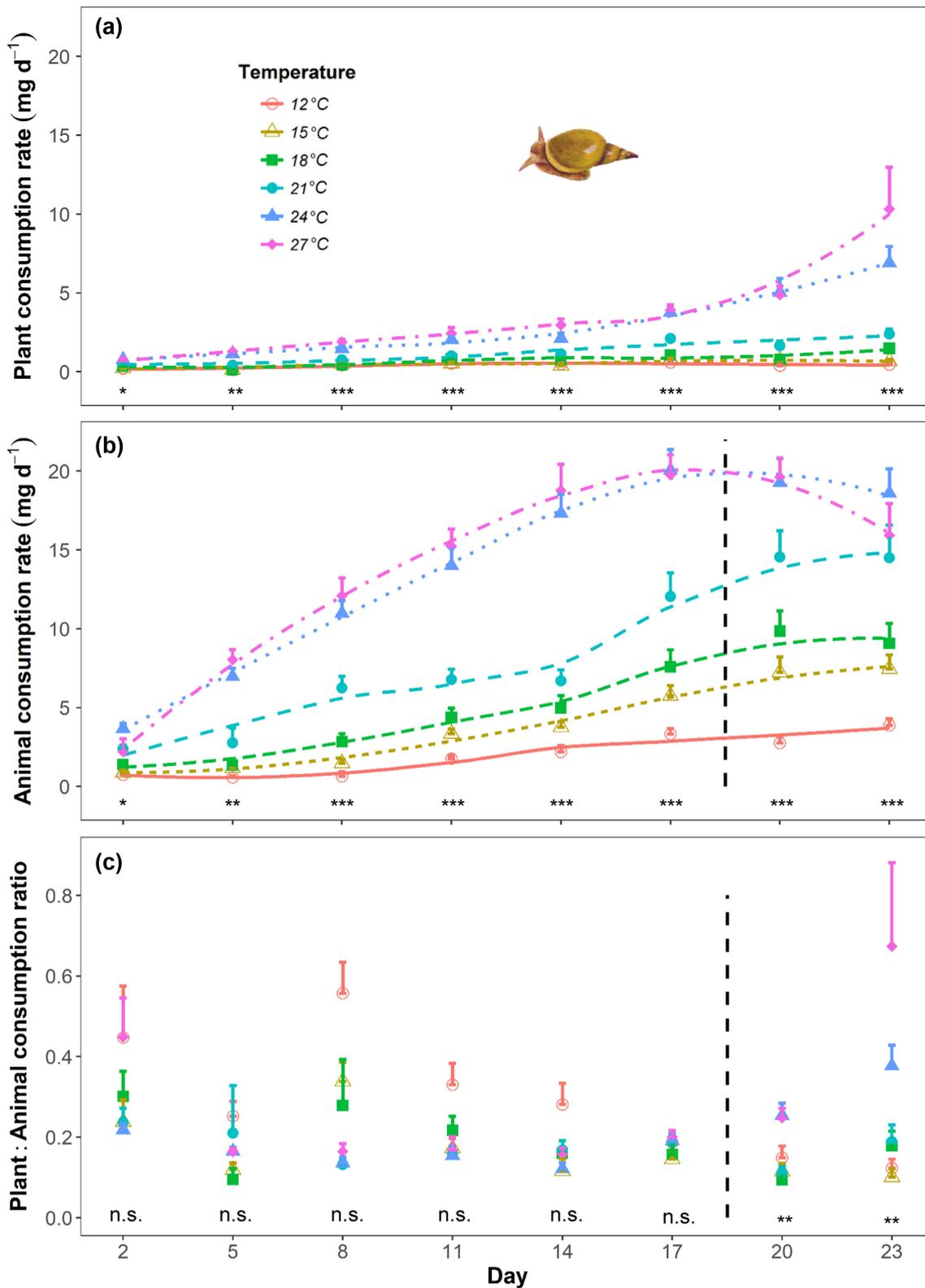


Figure 2. Temperature effects on pond snail food consumption rates and diet selection during the choice experiment. (a) Plant food consumption rates by snails; (b) Animal food consumption rates by snails; (c) Plant:animal food consumption ratios during the experiment. Dashed vertical lines indicate the diet shift time point. Standard errors are indicated by vertical bars (n = 8). Each data point represents the mean value over the three days of measurement and is displayed at the middle day. Statistical results are shown in the figures. 'n.s.' represents no significant effects at  $p > 0.05$ ; \* indicates  $p < 0.05$ ; \*\* indicates  $p < 0.01$ ; and \*\*\* indicates  $p < 0.001$ .

Table 2. Time and temperature effects on pond snail food consumption. Bold numbers indicate  $p < 0.05$ .

Parameters	Factors	numDF	denDF	F	p
Plant food consumption rate	Time	1	334	73.7	< <b>0.001</b>
	Temperature	1	10	5.5	<b>0.041</b>
	Time × Temperature	1	334	257.7	< <b>0.001</b>
Animal food consumption rate	Time	1	334	27.1	< <b>0.001</b>
	Temperature	1	10	101.3	< <b>0.001</b>
	Time × Temperature	1	334	4.9	<b>0.028</b>
Plant:animal consumption ratio	Time	1	334	35.5	< <b>0.001</b>
	Temperature	1	10	13.0	<b>0.005</b>
	Time × Temperature	1	334	27.5	< <b>0.001</b>

quality among seasons (Guinan Jr et al. 2015, Boersma et al. 2016, González-Bergonzoni et al. 2016). In addition, there may be an unknown bias against publishing non-significant results. Whereas most studies confirmed our hypothesis, there were still two cases that did not find temperature effects on aquatic omnivorous diet selection (Table 3).

The first case was that adult crayfish did not increase the proportion of plant material in their diet with rising temperatures (Carreira et al. 2017). However, the parallel study using juvenile crayfish found a trend of increasing herbivory with rising temperatures. Crayfish have been shown to increase herbivory with increasing age (Momot 1995), which indicates that rising temperature might enhance the growth of crayfish and increase herbivory. The second case was that the adult pond snail did not increase herbivory with rising temperatures in a 24h diet selection experiment (Zhang et al. 2018b). However, in a longer term, the juvenile pond snail in our study increased herbivory at higher temperatures after 17 days. These two cases do not reject our hypothesis, but rather suggest that this hypothesis might depend on the life stage and experimental duration, at least for some species.

Our snail experiment is the first to quantify the diet selection of juvenile ectotherm omnivores over time. The snails at higher temperatures reached 2.4 cm shell length and the growth levelled off from 24°C at the end of the experiment (Fig. 3), indicating that the snails reached adulthood (Van

der Schalie and Berry 1973, Elger and Barrat-Segretain 2002, Koene et al. 2006). This means that the diet shift of the snails after 17 days at higher temperatures could be due to the ontogenetic development of the snails, namely the snails may have shifted their diet when they become adults. This extrapolation is also supported by the study which tested the diet selection of adult pond snails in a 24h feeding trial, but did not find differential diet selection at higher temperatures (Zhang et al. 2018b). Animals often have different nutrient demands at different life stages (Stockhoff 1993, Urabe and Sterner 2001, Claes and Maarten 2003, Bullejos et al. 2014, Richard et al. 2018). Animal food has a higher nutrient content compared to plant material (Elser et al. 2000, Zhang et al. 2018c), as also shown in our study. Juveniles might need food with a lower C:nutrient ratio than their conspecific adults, as they need more nitrogen and phosphorous for their growth, leading to an ontogenetic shift in stoichiometric demand (Nakazawa 2011, Bullejos et al. 2014, Boros et al. 2015). Many aquatic omnivores increase the proportion of plant material in their diet during their ontogenetic development (Werner and Gilliam 1984, German and Horn 2006, Burgett et al. 2018). At high temperatures, animals grow faster and mature earlier, resulting in a smaller final body size (Kingsolver and Huey 2008, Daufresne et al. 2009), and accrue relatively less nutrients in their bodies (Woods et al. 2003). Thus, they might shift their diet earlier

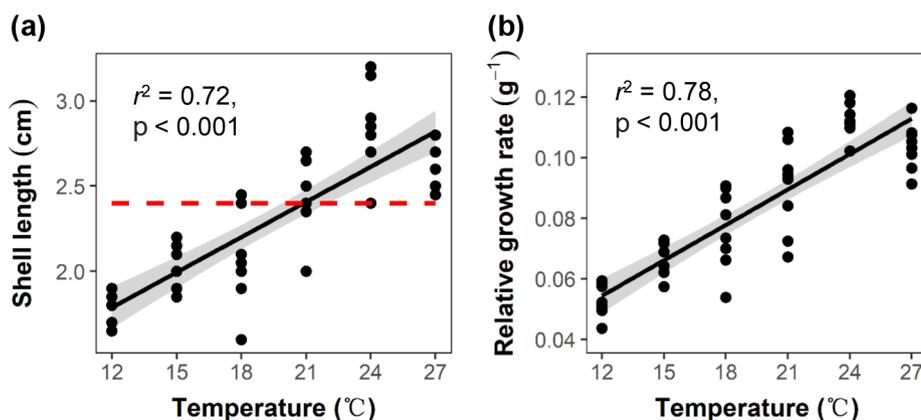


Figure 3. Temperature effects on snail growth parameters in the experiment. (a) Final shell length and (b) Relative growth rate. Temperature effects on the growth parameters were tested by linear mixed effects models, and results are indicated in the plot. Dashed horizontal red line (shell length = 2.4 cm) indicates the threshold above which snails are generally sexually mature (Van der Schalie and Berry 1973, Elger and Barrat-Segretain 2002, Koene et al. 2006).

Table 3. Results of studies which investigated rising temperature effects on diet selection of aquatic omnivores.

Taxon	Omnivore	Plant food	Animal food	Experiment approach	Quantified methods	Time	Temperature range	Results	Reference
Zooplankton	Copepod ( <i>Temora longicornis</i> )	Cryptophyte ( <i>Rhodomonas salina</i> )	Dinoflagellate ( <i>Oxyrhis marina</i> )	Seasonal comparison	Stable isotope method	–	3–23°C	Decreased trophic position with rising temperature	Boersma et al. 2016
Amphibian	Tadpole ( <i>Discoglossus gaiganoi</i> )	Macrophyte ( <i>Juncus heterophyllus</i> )	Chironomid larvae	Temperature manipulation	Quantify grazing rate	24 h	8–26°C	Preferred plant food at high temperature	Boersma et al. 2016
	Tadpole ( <i>Hyla arborea</i> )	Macrophyte ( <i>Ranunculus peltatus</i> )	Chironomid larvae	Temperature manipulation	Stable isotope method	2 months	17–25°C	Increased herbivory with rising temperature	Carreira et al. 2016
Crayfish	Tadpole ( <i>Hyla meridionalis</i> )	Macrophyte ( <i>Ranunculus peltatus</i> )	Ephemeroptera (mayfly) larvae	Temperature manipulation	Stable isotope method	2 months	17–25°C	Increased herbivory with rising temperature	Carreira et al. 2016
	<i>Procambarus clarkia</i> – juvenile	Macrophyte ( <i>Juncus heterophyllus</i> )	Chironomid larvae	Temperature manipulation	Stable isotope method	2 months	17–25°C	Tendency of increasing herbivory with warming	Carreira et al. 2017
	<i>Procambarus clarkia</i> – adult	Macrophyte ( <i>Juncus heterophyllus</i> )	Chironomid larvae	Temperature manipulation	Stable isotope method	2 months	17–25°C	No temperature effects on preference	Carreira et al. 2017
Fish	Rudd <i>Scardinius erythrophthalmus</i>	Macrophytes	–	–	Gut content analysis	–	15–23°C	Increased plant consumption as temperature increased	Prejs 1984
Snail	Opaleye <i>Girella nigricans</i>	Algae ( <i>Ulva</i> spp.)	Squid pieces	Temperature manipulation	Quantify performance	28 days	12–27°C	Increased performance at low temperature feeding on animal food	Behrens and Lafferty 2007
	<i>Bryconamericus iheringi</i>	Filamentous algae	Tubificid worms	Seasonal comparison	Gut content analysis	4 days	10–22°C	Increased herbivory in summer	González-Bergonzoni et al. 2016
	Rudd <i>Scardinius erythrophthalmus</i>	–	–	Seasonal comparison	Stable isotope method	–	9–25°C	Increased herbivory in summer	Guinan Jr et al. 2015
Cichlids	Rudd <i>Scardinius erythrophthalmus</i>	Macrophyte ( <i>Potamogeton pectiatus</i> )	Chironomid larvae	Temperature manipulation	Gut content analysis	24 and 168 h	13–24°C	Increased herbivory with rising temperature	Vejříková et al. 2016
	<i>Cichlids (Amatitlania nigrofasciata)</i>	Plants	Molluscs, insects, crustaceans	Field comparison	Gut content analysis	–	27–31°C	Increased herbivory at higher temperature	Emde et al. 2016
	Pond snail ( <i>Lymnaea stagnalis</i> , adult)	Macrophyte ( <i>Potamogeton lucens</i> )	Amphipod ( <i>Cammarus pulex</i> )	Temperature manipulation	Quantify feeding rate	24 h	15–25°C	No temperature effects on preference	Zhang et al. 2018b
Pond snail ( <i>L. stagnalis</i> , juvenile)	Macrophyte ( <i>Elodea nuttallii</i> )	Chironomid larvae	Temperature manipulation	Quantify feeding rate	23 days	12–27°C	Increased herbivory at higher temperature after 17 days	This study	

from food with a lower C:nutrient ratio to food with a higher C:nutrient ratio with increasing temperature, which can be achieved by increasing herbivory at higher temperatures.

Life stages and variation in ontogenetic stoichiometry demand during different life stages of animals have so far been completely neglected in the previous hypotheses. We here propose to include the ontogenetic development in the TMSH hypothesis to explain the possible diet shift of omnivores with rising temperature (Fig. 1). However, for the ectotherms with metamorphose or multiple life stages, their nutrient demands vary discretely at different life stages (Werner and Gilliam 1984, Stockhoff 1993, Boros et al. 2015). Hence, the diet shift of omnivores might occur multiple times during their lifetime, changing with their growth, reproduction and senescence. We did not test these in our experiment, and this would be something interesting to explore in the future. Therefore, there is not a universal simple rule which can be applied to all cases; instead more studies are needed that test diet selection of omnivores at different life stages over similar time scales to verify the hypotheses.

### Implications of increased herbivory under climate change

As global temperatures increase, this might change the ratio of available food items. In nature, omnivorous diet selection also depends on food availability (Guinan Jr et al. 2015, Vejříková et al. 2016), as animal food is not always as abundant as plant material. If there is no animal food available, omnivorous animals might become herbivores, and they might need to consume more plant material to compensate for their nutrient demand due to the lower nutrient content of plant material (Cruz-Rivera and Hay 2000, Fink and Von Elert 2006). This will lead to enhanced top-down pressure on primary producers by herbivory with warming (Fig. 4a–b), as ectothermic animals increase their metabolic rates with rising temperature resulting in higher consumption rates. When there is animal food available, the omnivores might increase the proportion of plant material in their diet with warming (Fig. 4c–d). Together these changes in consumption rates and food availability suggest that future climate change might lead to stronger grazing pressure on primary producers, by both herbivores and omnivores.

In addition, with rising temperature, the omnivores might grow faster and shift earlier to increase plant consumption and establish larger population sizes leading to more consumption of primary producers (Meerhoff et al. 2007, Jeppesen et al. 2010, González-Bergonzoni et al. 2012, O’Gorman et al. 2017). Furthermore, the consumption rate of animals might increase faster than the biomass accumulation rate of primary producers with rising temperature (O’Connor 2009, Gilbert et al. 2014, West and Post 2016, Schaum et al. 2018). These findings indicate that the top-down control on primary producers by herbivory of ectothermic omnivores might be even stronger in nature under future warming and heatwaves. However, where the tipping point for the diet shift is, and when this will happen, has

implications for the impacts of future climate change. The increased degree of herbivory with rising temperature will strengthen the omnivorous interaction between primary producers and consumers, which might lead to an unstable food web (Wootton 2017). Therefore, a shift in diet selection by omnivores due to climate change might first alter the relative and absolute abundance of primary producers and animal prey, then followed by a collapse of the community of omnivores and the food web.

### Future studies

Clearly, more studies are needed to enable better predictions on the effects of global warming on plant consumption in aquatic systems. We here list four key directions.

1. Although aquatic ectothermic omnivores seem to generally increase herbivory with rising temperature, the underlying mechanisms are still unclear. Explanations from the aspects of temperature effects on animal physiology, metabolism and stoichiometric demands could not fully clarify why ectothermic omnivores increase herbivory with rising temperature. We here propose to additionally take the animal ontogenetic diet shift into consideration when interpreting diets shift by omnivores. More experiments are needed to verify the various hypotheses.

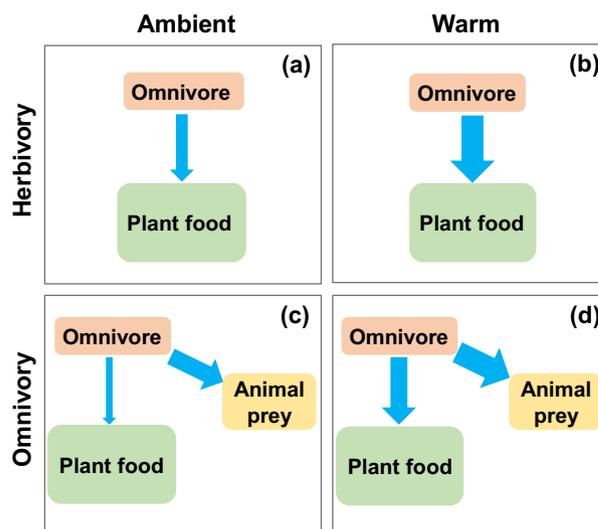


Figure 4. Proposed implications of warming effects for plant consumption by ectotherm omnivores in the absence and presence of animal prey. The omnivore is an animal that could consume both plant material and animal food. When there is no animal prey, the omnivore behaves as an herbivore and has a stronger top-down effect on the plant food in warm (b) compared to ambient (a) scenarios by increasing its consumption rate. When there is animal prey, the consumer behaves as an omnivore and when changing from an ambient (c) to a warm (d) scenario, the omnivore increases its consumption rate, thereby consuming more animal prey, but also increases its preference for plant food, thereby increasing the top-down effect on plant food. Arrows indicate the top-down effect. Width of the arrows indicates their magnitude.

2. Compared to several other studies, our study was performed in a more direct way. We measured the omnivore consumption rates on both types of food over time, whereas other studies employed stable isotope methods (Guinan Jr et al. 2015, Boersma et al. 2016, Carreira et al. 2016, 2017). The stable isotope method has been used to indicate the food assimilation, which is not equal to consumption (Boecklen et al. 2011). Both methods have their own strengths. Whereas isotope studies can better indicate which type of food could be utilized best by omnivores, our study can better indicate better the amount of plant consumption, which is important to assess direct top-down grazing pressure of omnivores on primary producers. Future studies should test more ectothermic omnivores in long-term diet-selection experiments at multiple life-stages at different temperatures. Furthermore, multiple plant material should be tested to generalize the conclusions, and also agar food composed with manipulated nutrients is a very relevant approach. Agar-based food eliminates the physical structure of natural food material, which allows to focus on the nutrient composition of the food.
3. Even though multiple studies have found that warming might increase herbivory by aquatic omnivores, there is still no study that explored the consequences of this diet shift for the impact of omnivores on the abundance or diversity of primary producers at either the community or ecosystem level. Similarly, studies on the impact of warming through increased herbivory by omnivores are lacking in terrestrial ecosystems. Therefore, more studies are needed to test the effects of warming on primary producers via increased herbivory, taking into account more complete and thus more realistic food webs.

### Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.fj6q573qv>> (Zhang et al. 2020).

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*Author contribution* – PZ and ESB formed the idea of the research. PZ, CHAL, DB, MP and ESB designed the experiment. PZ, DB

and MP performed the experiment. PZ, CHAL and JX did the data analysis. PZ, CHAL, DB, MP, JX and ESB wrote and revised the paper.

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Supplementary material (available online as Appendix oik-07082 at <[www.oikosjournal.org/appendix/oik-07082](http://www.oikosjournal.org/appendix/oik-07082)>). Appendix 1.