



# Larger crustacean zooplankton thrive at lower temperatures and under reduced predation in pond ecosystems

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**Abstract** Body size is a fundamental trait influencing ecological functions, trophic dynamics, and organismal fitness across ecosystems. However, the environmental drivers shaping body size patterns in pond ecosystems across broad spatial scales remain poorly defined. In this study, we assessed the main determinants of body size in cladocerans and copepods, key crustacean zooplankton groups, across 168 ponds including regions in Europe, Asia, and South America. We assess how temperature

and latitudinal variation, food availability, and predation influence mean and maximum crustacean body sizes in zooplankton taxa. Using linear mixed models, we identified annual temperature and predation pressure as the strongest predictors of body sizes. Body size increased with lower temperature for both taxa, supporting the temperature-size rule. Fish presence was associated with smaller body sizes for both taxa, while copepod size metrics were additionally influenced by pond morphology, showing a negative relationship with depth and a positive association with area. These findings suggest temperature and predation pressure act as major selective forces shaping crustacean body size in pond ecosystems. Understanding these patterns is essential for predicting how crustacean communities and processes they mediate may respond to ongoing climate warming, particularly in

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small-shallow freshwater ecosystems highly sensitive to environmental change.

**Keywords** Latitude · Shallow freshwater ecosystems · Resource availability · Cladocera · Copepoda · Wetlands

## Introduction

According to the Metabolic Theory of Ecology, temperature is the primary abiotic driver of metabolism, as higher environmental temperatures accelerate biochemical reactions by increasing molecular kinetic rates which, in ectothermic organisms, can reduce lifespan and increase mortality under stressful conditions (Gillooly et al., 2001; Brown et al., 2004). Another important key consequence is the reduction in body size, a widespread phenomenon described by the temperature-size rule (TSR), whereby individuals tend to be smaller in size at higher temperatures (Atkinson, 1994). The TSR reflects a phenotypic response to thermal conditions during development, as warmer temperatures increase both growth and development rates, ultimately resulting in smaller adult sizes (Atkinson, 1994; Ohlberger, 2013). This pattern has been observed across a wide range of aquatic taxa (Gardner et al., 2011; Forster et al., 2012), including phytoplankton (Daufresne et al., 2009), crustacean zooplankton (Gillooly, 2000; Daufresne et al., 2009;

Evans et al., 2020), and fish (Emmrich et al., 2014; Coghlan et al., 2024).

Body size is a master functional trait that integrates an organism's physiology, ecology, and fitness (White et al., 2007; Kiørboe, 2008), influencing processes from individual performance to ecosystem functioning (Brown et al., 2004, 2007; Woodward et al., 2005). In aquatic ecosystems, body size plays a particularly central role, structuring energy flow and trophic dynamics through both top-down and bottom-up processes (Shurin et al., 2005; Hildrew et al., 2007). Because many life-history traits scale with size, shifts in individual body size can cascade across levels of biological organization (Li et al., 2022; Albini et al., 2025). Therefore, identifying the main factors that shape body size in zooplankton is particularly relevant in the context of climate change, as it alters environmental conditions and ecological interactions.

Aquatic ecosystems, such as ponds, play a central role in global biodiversity despite their small size (Oertli et al., 2002; Williams et al., 2004) and contribute significantly to climate regulation, helping to mitigate global warming through carbon sequestration and other ecological functions (Céréghino et al., 2014; Cuenca-Cambronero et al., 2023). Their small area has historically led to their underrepresentation in ecological studies and conservation strategies, yet paradoxically, it also renders them highly vulnerable to anthropogenic stressors and climate warming (Oertli et al., 2005; Hill et al., 2021; Fluet-Chouinard et al., 2023). In the context of climate change, rising temperatures pose a multifaceted threat to pond ecosystems, not only by directly influencing the physiology and development of aquatic organisms, but also by indirectly restructuring food web dynamics (Deutsch et al., 2022). Warming can simultaneously intensify top-down and bottom-up processes, altering resource availability, modifying predator–prey interactions, and shifting the balance of consumer-resource dynamics, thereby disrupting ecological stability (Moore et al., 1996; Shurin et al., 2012; Deutsch et al., 2022). These indirect effects are further compounded by the temperature-dependent metabolic responses of organisms, which vary across environmental conditions, leading to context-specific outcomes. As a result, warming can trigger cascading effects that reshape community composition and

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impact broader ecological processes, including productivity, nutrient cycling, and trophic dynamics (Brown et al., 2004; Ohlberger, 2013; Saito et al., 2021). Notably, most empirical evidence for such warming-driven cascading effects comes from ecosystems other than ponds (Woodward et al., 2010; Woolway et al., 2022), highlighting the need to investigate whether similar patterns occur in pond systems.

A particularly relevant group for exploring these temperature–body size relationships is crustacean zooplankton. Zooplankton species are particularly important as they are a central part of the food web of aquatic ecosystems, feeding on phytoplankton and bacterial communities, but also being the main prey for higher trophic levels such as macroinvertebrates and fish (Brooks & Dodson, 1965; Litchman et al., 2013). Through these interactions, zooplankton link the classical food web with the microbial loop and contribute to nutrient recycling (Segovia et al., 2015). In warm water, zooplankton tend to be smaller than in cold water (Burton & Einum, 2020; Evans et al., 2020; Albin et al., 2025). This pattern has been attributed mainly not only to changes in temperature (Gillooly, 2000; Gillooly & Dodson, 2000; Havens et al., 2015; Horne et al., 2016), but also to food resource availability, specifically through the higher density of large inedible algae and lower density of smaller edible algae (Jeppesen et al., 2000; Lefort et al., 2015), and fish predation, which disproportionately targets larger zooplankton (Brooks & Dodson, 1965; Meerhoff et al., 2007a; Brucet et al., 2010; Iglesias et al., 2011; das Candeias et al., 2022).

Large-scale studies on crustacean body size in natural aquatic ecosystems across broad latitudinal and thermal gradients were mainly focused on evaluating the effects of temperature on body size, either through meta-analyses (Gillooly & Dodson, 2000; Horne et al., 2016), empirical studies in lakes (Gyllström et al., 2005; Havens et al., 2015) or in marine ecosystems (Evans et al., 2020), and laboratory experiments (Horne et al., 2015). Overall, these studies supported the temperature-size rule, showing a consistent pattern of decreasing body size with increasing temperature. However, taxon-specific responses have also been observed in crustacean zooplankton as Havens et al. (2015) reported a marginal decrease in body size with an increase in temperature in cladocerans,

a more pronounced decline in cyclopoid copepods, and no significant effects on calanoid copepods, highlighting the complexity of temperature effects across different crustacean groups.

Notably, most of these studies have focused solely on thermal gradients, leaving a gap in our understanding of how other ecological drivers (i.e., predation pressure or food resource availability) may also shape body size patterns at broad spatial scales in natural ecosystems. For instance, using freshwater mesocosms, Kratina et al. (2012) showed that warming can intensify trophic cascades, strengthening top-down control by fish and reducing bottom-up regulation by nutrients on primary producers. This result suggests that higher temperatures may strengthen predation effects and weaken nutrient-driven productivity, with potential consequences for body size structure across trophic levels. Supporting the top-down perspective, some studies suggest that fish predation pressure is a key driver of body size along latitudinal gradients (Brucet et al., 2010; Iglesias et al., 2011). These changes can affect crustaceans, both through increased predation pressure from fish and through changes in food availability. Warming is often associated with shifts in phytoplankton communities toward smaller, less nutritious taxa such as cyanobacteria, which tend to dominate under high temperatures, form dense blooms, and reduce food quality and quantity for crustacean grazers due to their poor nutritional value and low edibility (Yvon-Durocher et al., 2011). In this context, both top-down (predation) and bottom-up (resource availability and quality) mechanisms may interact to shape crustacean body size patterns.

Disentangling the relative influence of environmental drivers such as temperature, food resource availability, and predation on crustacean body size in pond ecosystems is key to understanding the distribution and functional role of crustacean body size in aquatic ecosystems. Here, we present a study based on 168 shallow ponds distributed along broad climatic regions across four European countries (Spain, Germany, Belgium, and Denmark), Türkiye, and South America (Uruguay). Our aim was to assess the variation in individual body size of crustacean cladocerans and copepods across a latitudinal gradient and to identify its main drivers. Thus, for each pond, we calculated three body size metrics for cladocerans and copepods as response variables:

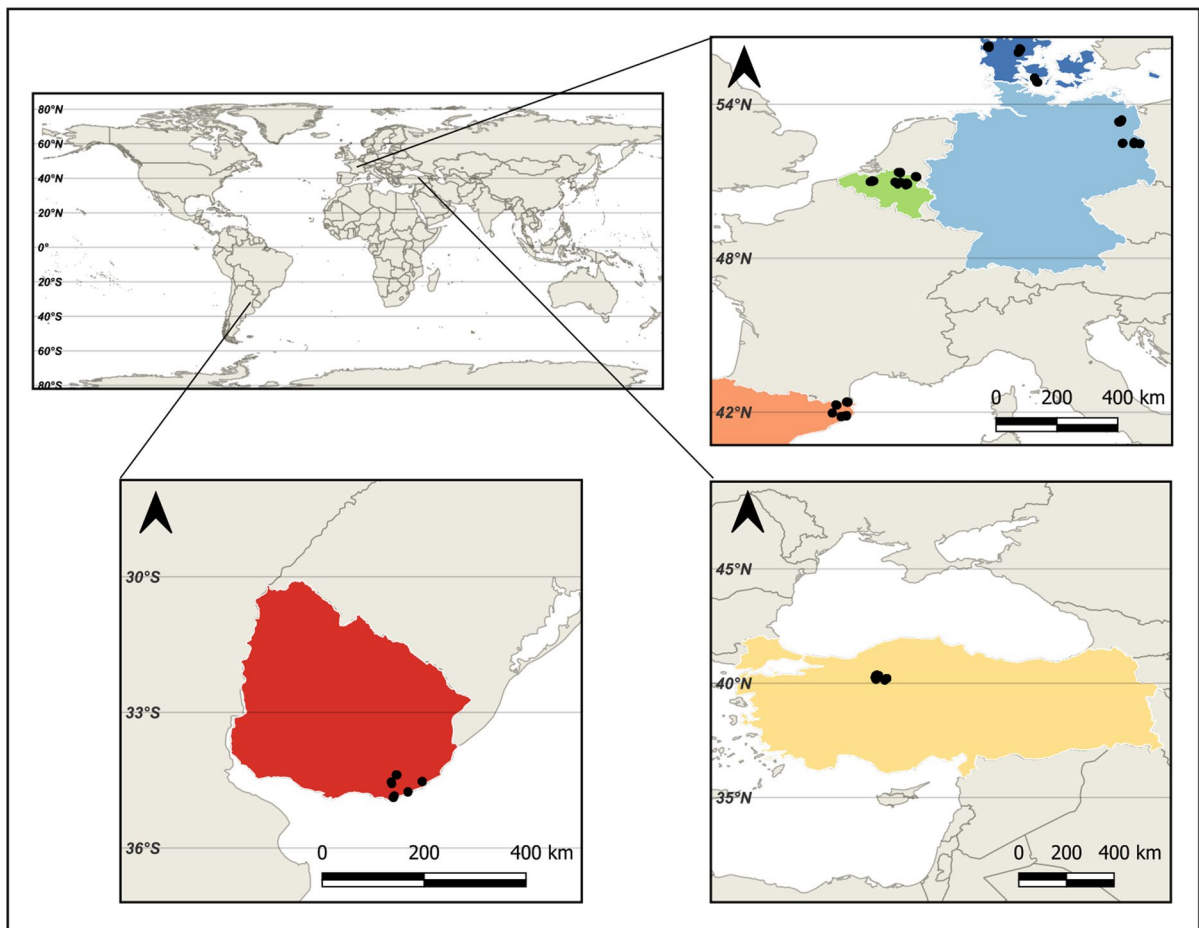
arithmetic mean, geometric mean, and maximum size. We predicted that (i) body size for each crustacean group would decrease toward higher temperatures, reflecting the general trend of smaller sizes in warmer environments; (ii) body size would decline in the presence of fish and with increased abundance of macroinvertebrate predators; and (iii) body size would increase with greater food availability, as more abundant resources support the growth of larger individuals. In addition, to account for potential confounding effects of pond morphometry, we included pond area and depth into our analyses. By addressing these hypotheses, we aim to contribute to a better understanding of the main drivers of

crustacean zooplankton body size variation in ponds under changing environmental conditions.

## Material and methods

### Study area

Data were collected from a total of 245 surveys in 168 ponds distributed across four European countries: Denmark (40), Belgium (39), Germany (42), Spain (42), as well as from the Asian part of Türkiye (42), and from Uruguay (40) in South America. This dataset spans from  $-34.88^{\circ}$  to  $56.28^{\circ}$  (Fig. 1), covering



**Fig. 1** Geographic distribution of the study sites across Europe, South America, and Asia. The large map displays the global context, highlighting the sampled countries. The top-right inset focuses on European sites: Spain (orange), Belgium (green), Germany (light blue), and Denmark (dark blue). The

bottom-left inset shows Uruguay (red) in South America, while the bottom-right inset highlights Türkiye (yellow) in the Middle East. Black circles within each highlighted country indicate the sampling locations

temperate, Mediterranean, continental dry, and cold semi-arid and subtropical climates with no representation of tropical latitudes ( $-30^{\circ}$  to  $30^{\circ}$ ). Ponds within each country were selected using a stratified design that considered gradients of trophic state and two hydrological regimes: permanent (178) and temporary (67). We considered temporary ponds those that dry every year, whereas permanent ponds were those that do not dry. All ponds were located in lowland ( $<800$  m. a.s.l) and rural areas. Detailed information on the geographic coordinates (latitude and longitude) for each country is provided in supplementary materials 1. We followed the same criteria for pond selection and characterization as described in Bartrons et al. (2025), López-de Sancha et al. (2025a) and Rincón-Palau et al. (2025).

### Data collection and sampling

Sampling was conducted over two consecutive years (Bartrons et al., 2025; Rincón-Palau et al., 2025) during spring/summer for each country. In European countries and Türkiye, sampling was carried out between April and July, whereas in Uruguay, sampling was conducted between November and December. Due to delays caused by the COVID-19 pandemic, ponds in Türkiye were sampled in 2022 and 2023. During the first year of sampling, 2021 (or 2022 in the case of Türkiye), approximately 30 ponds per country were sampled, while in 2022 (2023 for Türkiye), a selection of 10 to 12 ponds from the first sampling campaign were sampled again.

Chlorophyll-a (Chl-a) concentration, used as a proxy of food resource availability for crustacean zooplankton, was measured *in vivo* with a portable fluorometer. Chl-a is a standard and widely used proxy of phytoplankton biomass (Aranguren-Riano et al., 2011; Escribano et al., 2016; Suchy et al., 2022; Wang et al., 2023), and consequently, for food resource availability for crustacean zooplankton. However, Chl-a does not fully capture its dietary diversity (e.g., for omnivorous and carnivorous zooplankton taxa). The mean water column depth was measured along two perpendicular transects at 2-m intervals using a graduated stick inserted perpendicularly to the bottom of the pond (supplementary material 2). The pond surface area was estimated from Google Earth (supplementary material 2). As a climatic variable, we calculated the average air temperature over the three

months preceding each sampling event, as this period is crucial for zooplankton development and helps minimize the influence of seasonal temperature fluctuations. In addition, we calculated the annual average air temperature for each sampling year. Temperature data were obtained from the NASA POWER (<https://power.larc.nasa.gov/data-access-viewer/>). For further details on sampling and collection of physicochemical variables, as well as other parameters relevant for pond characterization, see also Bartrons et al. (2025) and Rincón-Palau et al. (2025).

To estimate the influence of zooplankton's potential predators, we assessed fish presence/absence through eDNA metabarcoding following Brys et al. (2021) in European countries and Türkiye, while in Uruguay, we used electrofishing. For fish eDNA analyses, water samples were collected from each pond at multiple locations and microhabitats using a pole with a sterile Whirl-Pak sampling bag attached to it and then filtering water (250 mL to 1 l) with 0.45- $\mu$ m pore size PVDF Sterivex-HV filter capsule (SVHVL10RC, Merck Millipore). For eDNA methodology details, see López-de Sancha et al. (2025a) and (2025b). Although not all fish species exert the same predation pressure on zooplankton, all detected species (supplementary material 3) were included in our analysis since most fish are zooplanktivorous at some stage of their life cycle, particularly during the juvenile stage (Wong & Ward, 1972; Hansen & Wahl, 1981; López-de Sancha et al., 2025a). All countries included ponds with and without fish, ensuring a representative distribution across the study area (supplementary material 2).

To estimate the total biomass of potential macroinvertebrate predators, we considered Odonata families and, for Coleoptera, we included larvae and adults of Dytiscidae and Noteridae, as well as Hydrophilidae larvae. Samples were collected using 20 sweeps with a sweep net per pond (mesh size: 500  $\mu$ m, frame size 25\*18 cm) across different meso-habitats. The samples were preserved in 70% ethanol. The body size of ten random individuals per taxon (identified at genus level for larvae and species level for adults) was measured, and biomass dry mass ( $\mu$ g/l) was then calculated following Benke et al. (1999).

Cladoceran and copepod samples were collected in a depth-integrating sample with a tube sampler from different locations within each pond to cover habitat heterogeneity. After sample homogenization, 40 l of

water was filtered through a 53- $\mu\text{m}$  mesh in European countries and Türkiye, and a 60  $\mu\text{m}$  mesh in Uruguay. Samples were preserved with Lugol solution (4%). The first 20 individuals for each taxon were measured (when possible), including both juveniles and adults for cladocerans. For copepods, 20 nauplii larvae were measured separately from copepodites and adults. In total, the dataset comprises 24,440 crustacean size measurements, of which 10,221 corresponds to cladocerans and 14,219 to copepods.

### Data analysis

To assess latitudinal variation in individual cladoceran and copepod body size and identify its environmental drivers, we split the database in two subsets, one for cladocerans and one for copepods, and analyzed each subset separately. For some countries, the number of ponds used for the analyses differed slightly between cladocerans and copepods because in some cases, the abundances were too low to calculate the size metrics (see supplementary material 2).

For each crustacean taxonomic group, we calculated three individual body size metrics: arithmetic mean, geometric mean, and maximum size, based on individual measurements. The arithmetic mean provides a simple and intuitive measure of the average individual body size. However, it is sensitive to outliers, that is, a few unusually large individuals can disproportionately raise the mean, especially in communities with skewed size distributions. The geometric mean, on the other hand, is less affected by extreme values and gives more balanced weight to all sizes, making it more appropriate when size distributions are right-skewed or approximately log-normal, as is often the case in zooplankton (Brucet et al., 2010). It is additionally considered the better measure of central tendency for non-normally distributed variables, as it more accurately reflects the central size of individuals in such distributions. Maximum body size was estimated as the 95th percentile rather than the absolute maximum to reduce outlier effects and provide a more robust representation of the upper size range of typical individuals. Maximum body size is linked to the presence of large individuals in the community, and can also reflect the presence of ecological pressures such as predation (Brooks & Dodson, 1965), not captured by average-based metrics.

To identify relationships between the three size metrics and local environmental and biotic factors, we used linear mixed-effects models (LMMs). As response variables, we considered the arithmetic mean body size, geometric mean size, and maximum size. As explanatory variables, we included: (1) chlorophyll-a concentration (Chl-a) as a proxy for food resource availability, (2) fish presence/absence and total biomass of potential macroinvertebrate predators as indicators of predation pressure, (3) annual average air temperature as geographical and climatic factor, and (4) pond surface area and mean water depth as morphometric variables.

Before including variables in the models, we used the *bestNormalize* package (Peterson, 2021) to find and execute the best transformation for all continuous predictor variables to meet variance homogeneity assumptions and improve normality (Zuur et al., 2009). We checked for linearity among explanatory and response variables and for multicollinearity by Pearson's correlation (supplementary material 4 and 5). Based on correlation analysis, explanatory variables with high collinearity ( $r > 0.6$ ) were excluded from the models. The three months average air temperature was removed due to its strong correlation with annual average temperature. Thus, the following variables were retained for the model construction: Chl-a, annual average of air temperature, fish presence/absence, macroinvertebrate predator biomass, pond surface area, and mean depth. Since the annual average air temperature was correlated with absolute latitude, we also tested alternative models using absolute latitude instead of temperature. By using absolute latitude, we aimed to capture this latitudinal gradient by measuring distance from the equator, regardless of hemisphere.

All continuous predictor variables used in the analyses except absolute latitude were standardized prior to inclusion in the models using the "*scale ()*" function in R, to allow comparison of the relative importance of each predictor on the response variable, as reflected in the standardized regression coefficients ( $\beta$ -values). We used the "*dredge ()*" function from the *MuMIn* package (Bartón, 2023) for model selection. This function generates all possible submodels by removing predictor variables from a global model and ranks them based on Akaike's Information Criterion (AIC). The most parsimonious models were selected using the lowest AIC value (Akaike, 1974).

We also tested interactions among predictor variables to explore whether the effects of bottom-up (Chl-a) and top-down (fish and macroinvertebrate predators) controls on zooplankton body size varied along the latitudinal gradient or depended on the presence of higher trophic levels. We expected that latitudinal differences in temperature and seasonality could modulate the influence of fish (latitude  $\times$  fish presence/absence), that the role of invertebrate predators might change with latitude (latitude  $\times$  macroinvertebrate predator biomass), and that macroinvertebrates could exert stronger effects when fish were absent (fish presence/absence  $\times$  macroinvertebrate predator biomass). None of these interaction terms were statistically significant and were therefore not retained in the final models. We checked the absence of multicollinearity ( $VIF < 3$ ), and we examined the residual diagnostic plots to assess homoscedasticity. The normality of residuals was tested by Shapiro–Wilk’s test ( $p$  value  $< 0.05$ ). Partial residual plots were used to explore the relationship between significant predictors and the response variables, after accounting for the effects of the other covariates in the model.

We included “Pond” (referring to the identity of the pond) as a random effect in all LMMs to account for potential non-independence among repeated observations of the same ponds across years and the hierarchical structure of the data. All analyses and graphical outputs were performed with R version 4.3.1 (R Core Team, 2021). Linear mixed-effects models were fitted using the package *lme4* (Bates et al., 2015). Model diagnostics and the evaluation of model assumptions were carried out using the packages *car* (Fox et al., 2001) and *lmtest* (Zeileis & Hothorn, 2002). Correlations among predictors were assessed with the packages *corrplot* (Taiyun, 2025), *PerformanceAnalytics* (Peterson et al., 2024), and *Hmisc* (Jr, 2025). Partial effects of predictors were visualized using the *ggeffects* package (Lüdtke, 2018), and all graphical outputs were created using *ggplot2* (Wickham, 2016).

## Results

Across all ponds, the arithmetic mean body size and geometric mean body size were higher in cladocerans than copepods, while the maximum body size was similar between the two groups (Table 1). According

**Table 1** Summary of body size metrics for both crustacean groups, pooled across all ponds. Values shown (in mm) include the arithmetic mean, geometric mean, and mean of maximum sizes (95th percentile), each accompanied by their standard deviations (in parentheses)

	Arithmetic mean body size	Geometric mean body size	Maximum body size (95th percentile)
Cladocerans	0.62 ( $\pm 0.31$ )	0.55 ( $\pm 0.27$ )	1.13 ( $\pm 0.59$ )
Copepods	0.56 ( $\pm 0.22$ )	0.46 ( $\pm 0.19$ )	1.14 ( $\pm 0.51$ )

to AIC values, the most parsimonious models for the three size-related metrics of both crustacean groups included mean annual temperature and predation-related variables as significant predictors (Tables 2 and 3). As LMMs results for cladocerans and copepods had the same predictors using arithmetic and geometric means, in the main text, we present only the LMMs results based on the geometric mean, as it is considered a better estimator. All LMMs obtained for the arithmetic means are provided in Appendix Table 6.

For cladoceran body size metrics, results of LMMs showed that temperature and predation were the main significant predictors. Specifically, we found a significant negative association between mean annual temperature and both geometric mean body size and maximum body size, while the absence of fish showed a significant positive relationship with both metrics (Table 2, Fig. 2). Thus, larger cladocerans were observed in fishless ponds and at lower temperatures. For both size metrics, the standardized Beta coefficients showed that fish absence had a stronger positive effect than mean annual temperature. For maximum body size (calculated from the 95th percentile) model, the random effect of pond was significant, with pond variance of 0.113 and residual variance of 0.194 corresponding to an intraclass correlation coefficient (ICC) of 0.37. This indicates that more than one-third of the variation in maximum body size is explained by differences among ponds. No significant effects of food resources availability or pond morphometry were detected on the cladocerans body size metrics.

As with cladocerans, temperature and predation were the determinants of copepod body size metrics, with pond morphometry also emerging as a significant factor. Specifically, the geometric mean body

**Table 2** The most parsimonious Linear Mixed Models (LMMs) for cladocerans, including the predictors that contribute to the variations of the body size metrics: geometric mean body size and maximum body (95th percentile) size are shown

Response variable	Predictor	Beta Coefficient (Estimate)	Std. error	t-Value	p-Value	VIF	AIC
Geometric mean body size	Intercept	0.50	0.02	20.20	< <b>0.001</b>	–	43.93
	Pond depth	–0.03	0.02	–1.77	0.08	1.06	
	Mean annual temperature	–0.05	0.02	–2.74	<b>0.01</b>	1.08	
	Fish (absence)	0.13	0.04	3.19	<b>0.002</b>	1.14	
Maximum body size (95th percentile)	Intercept	1.01	0.05	18.61	< <b>0.001</b>	–	374.81
	Pond depth	–0.07	0.04	–1.71	0.088	1.08	
	Mean annual temperature	–0.12	0.04	–2.97	<b>0.003</b>	1.09	
	Macroinvertebrates predator biomass	0.06	0.04	1.50	0.136	1.07	
	Fish (absence)	0.29	0.09	3.26	<b>0.001</b>	1.18	

For each model, the Beta coefficient (Estimate) and standard errors (Std. error), *t-value*, significance (*p value*), AIC, and VIF are shown. Statistically significant *p values* are shown in bold. Predictor variables used in the models were mean annual temperature, Chl-a, the macroinvertebrate biomass of potential predators of zooplankton, fish presence/absence, surface area, and mean water depth

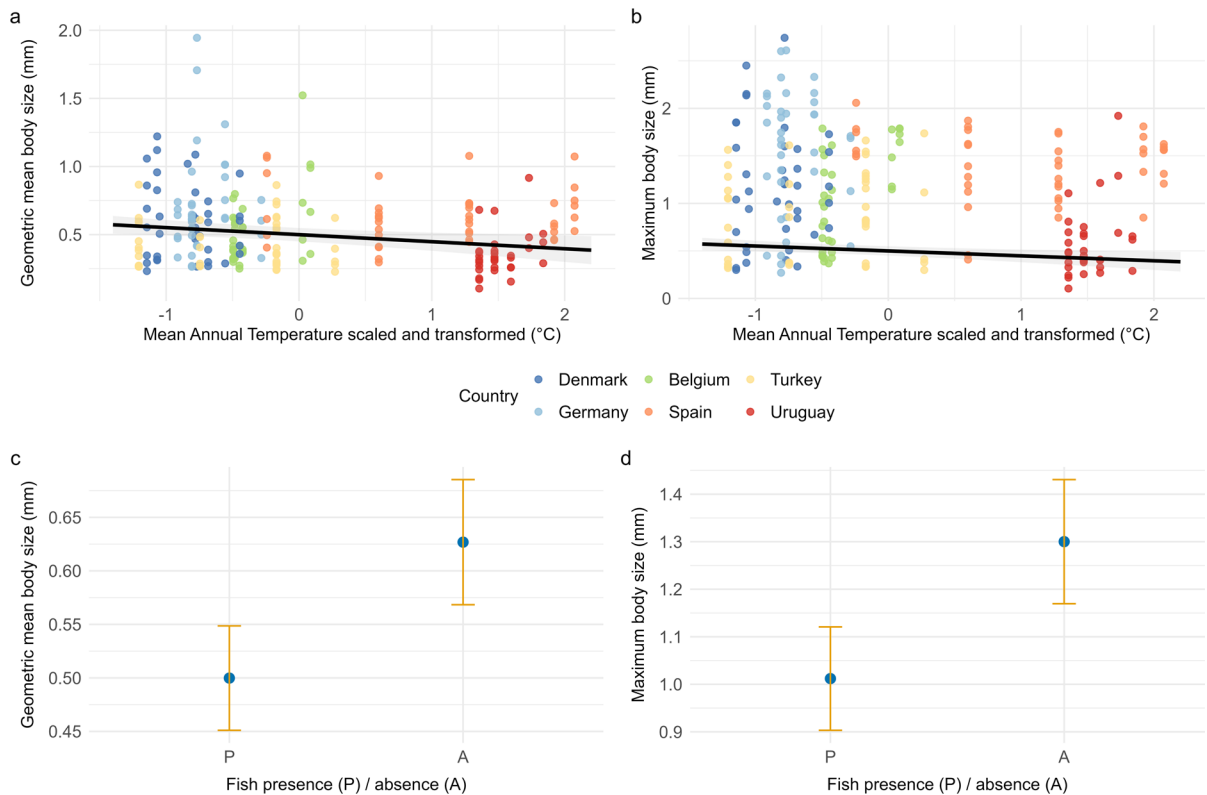
**Table 3** The most parsimonious Linear Mixed Models (LMMs) for copepods, including the predictors that contribute to the variations of the body size metrics: geometric mean body size and maximum body (95th percentile) size are shown

Response variable	Predictor	Beta Coefficient (Estimate)	Std. error	t-Value	p-Value	VIF	AIC
Geometric mean body size	Intercept	0.44	0.01	30.11	< <b>0.001</b>	–	–163.15
	Mean annual temperature	–0.10	0.01	–8.52	< <b>0.001</b>	1.06	
	Surface area	0.02	0.01	1.79	0.08	1.06	
	Pond depth	–0.02	0.01	–1.97	0.05	1.12	
	Fish (absence)	0.04	0.02	1.81	0.07	1.13	
Maximum body size (95th percentile)	Intercept	1.06	0.05	21.75	< <b>0.001</b>	–	333.91
	Mean annual temperature	–0.08	0.04	–2.13	<b>0.03</b>	1.07	
	Surface area	0.09	0.04	2.43	<b>0.02</b>	1.01	
	Fish (absence)	0.20	0.08	2.62	<b>0.01</b>	1.07	

For each model, the Beta coefficient (Estimate) and standard errors (Std. error), *t-value*, significance (*p value*), AIC, and VIF are shown. Statistically significant *p values* are shown in bold. Predictor variables used in the models were mean annual temperature, Chl-a, the macroinvertebrate biomass of potential predators of zooplankton, fish presence/absence, surface area, and mean water depth

size showed a significant negative relationship with mean annual temperature and a marginally significant relationship with pond depth, implying that copepods body size increases at lower temperatures and tends to be smaller in deeper ponds (Table 3, Fig. 3). Specifically, the standardized Beta coefficients revealed that mean annual temperature had a stronger effect than pond depth. For maximum body size, copepods showed a significant negative association with mean

annual temperature and significant positive associations with surface area and fish absence. Thus, largest copepods were observed in fishless ponds, in ponds with larger surface area, and at lower temperatures. The standardized Beta coefficients indicated that fish absence had the strongest effect, followed by pond surface area, with mean annual temperature having the smallest effect. Like cladocerans, copepod body



**Fig. 2** Cladocerans partial plots obtained from LMM models showing the relationship between response variables and the significant predictor variables after accounting for the contribution from other independent variables for a Partial effect of mean annual temperature on cladocerans' geometric mean body size. b Partial effect of mean annual temperature on cladocerans' maximum body size. c Partial effect of fish presence

(P)/absence (A) on cladocerans' geometric mean body size. d Partial effect of fish presence (P)/absence (A) on cladocerans' maximum body size. Plots show the linear regression (black line) with 95% confidence intervals, considering the contribution of all the variables included in the model. Mean annual temperature was previously transformed and standardized (scaled)

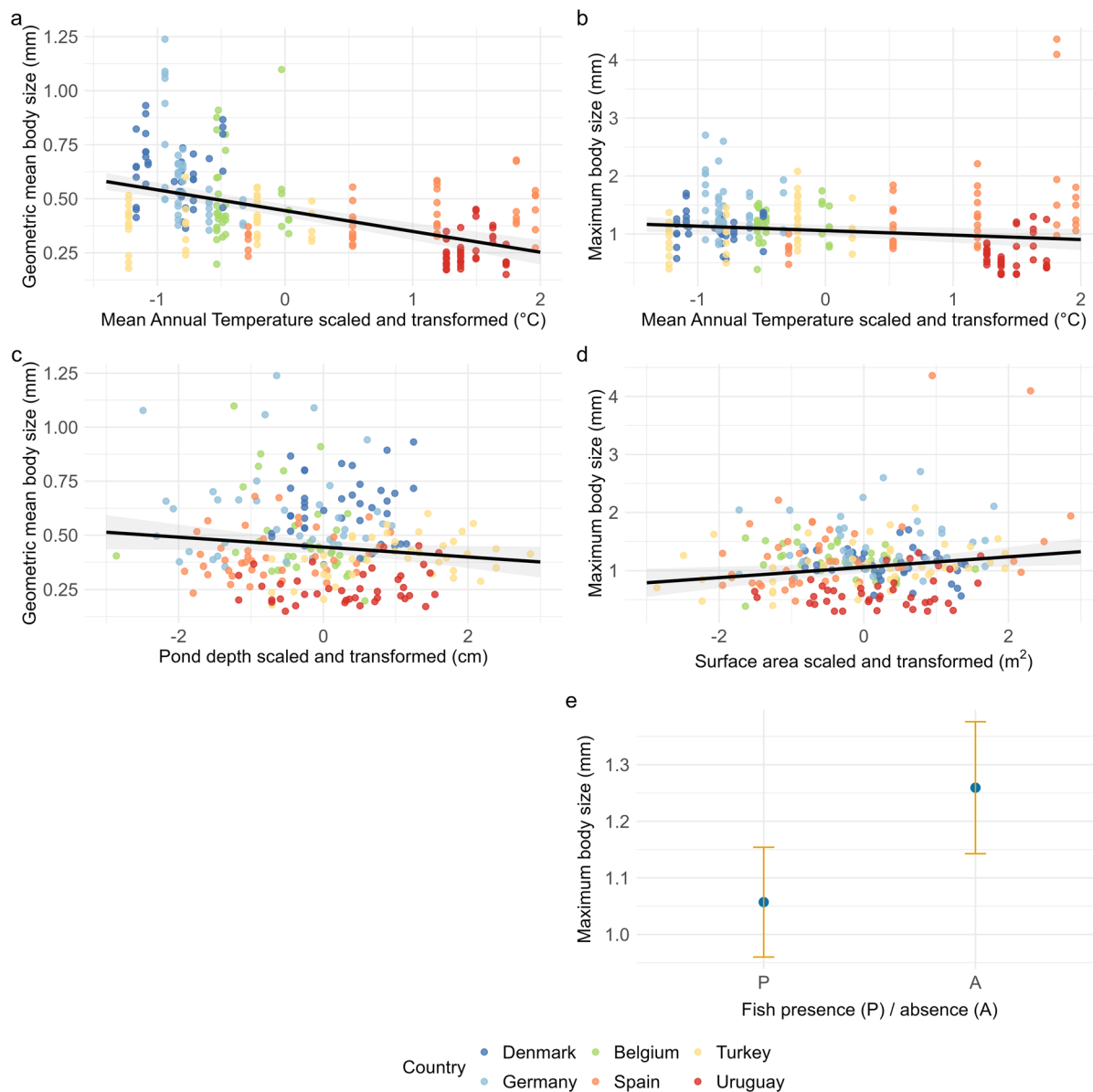
size metrics were not significantly influenced by food resource availability.

When absolute latitude was incorporated instead of mean annual temperature (to avoid collinearity) in the alternative LMMs (Appendix Tables 5 and 6), we found consistent patterns across taxa. In cladocerans (Appendix Table 5), both geometric mean and maximum body size increased with absolute latitude and in the absence of fish, suggesting that individuals tend to be larger at higher latitudes and under lower predation pressure. For copepods (Appendix Table 6), absolute latitude also showed a positive relationship with both size metrics. Geometric mean body size tended to increase with fish absence (marginal significance), while maximum body size was positively associated with both fish absence and pond surface area. Generally, sites located farther from the equator

presented larger zooplankton body sizes. Regarding the magnitude of predictors effects, fish predation had a stronger influence than latitude across all models, as indicated by the standardized Beta coefficients (Appendix Tables 5 and 6). As in alternative LMMs using temperature, no significant effects of food resource availability were observed on crustacean body size metrics.

## Discussion

Our study provides strong evidence supporting the hypothesis (i) that individual body size for crustacean cladocerans and copepods decreases toward higher temperatures, aligned with the temperature-size rule (TSR), which states that ectothermic organisms tend



**Fig. 3** Copepods partial plots obtained from LMM models showing the relationship between response variables and the significant predictor variables after accounting for the contribution from other independent variables for **a** Partial effect of mean annual temperature on copepods' geometric mean body size. **b** Partial effect of mean annual temperature on copepods' maximum body size. **c** Partial effect of pond depth on copepods' geometric mean body size. **d** Partial effect of sur-

face area on copepods' maximum body size. **e**. Partial effect of fish presence/absence on copepods' maximum body size. Plots show the linear regression (black line) with 95% confidence intervals, considering the contribution of all the variables included in the model. Mean annual temperature, pond depth, and surface area were previously transformed and standardized (scaled)

to attain larger body sizes in colder environments (Atkinson, 1994; Brown et al., 2004). This pattern was further supported by the significant positive effect of latitude found in our alternative models

(Appendix Table 5 and 6). Our findings are consistent with previous studies across aquatic taxa (Daufrès et al., 2009; Evans et al., 2020; Coghlan et al., 2024), including freshwater cladocerans (Gillooly

& Dodson, 2000; Havens et al., 2015) and copepods (Havens et al., 2015; Horne et al., 2016). By encompassing a broad latitudinal and climatic range (temperate, Mediterranean, continental semi-arid and subtropical climates), our results extend the applicability of the TSR to planktonic crustacean communities in pond ecosystems.

In addition to temperature and latitude, fish predation played a key role in shaping crustacean body size in ponds. In fact, as a general pattern, whenever fish absence was a significant predictor, its effect size was greater than that of the other variables. Thus, our results partially support the hypothesis (ii) which proposed that body size would decrease in the presence of fish and with higher abundance of macroinvertebrate predators. As a general pattern, fish presence was associated with significantly smaller body sizes (both geometric mean and maximum body size) in both crustacean groups, indicating strong top-down control likely driven by size-selective predation on larger individuals. These findings are consistent with established patterns of fish predation in planktonic communities, which disproportionately target larger zooplankton (Brooks & Dodson, 1965; Brucet et al., 2010; Iglesias et al., 2011). Nevertheless, the absence of a general significant effect of macroinvertebrate abundance (with only marginal significance in one model) suggests that macroinvertebrates did not act as size-selective predators on zooplankton in the studied ponds. This pattern could be explained by several factors. First, our analysis only included odonates and a limited number of coleopteran groups. Notonectids and other predatory taxa, not considered here, are known to exert strong size-selective predation on larger crustaceans (Herwig & Schindler, 1996; Shurin, 2001). This restricted taxonomic coverage may have underestimated the overall influence of macroinvertebrate predation and obscured possible size-selective effects on zooplankton body size. Second, environmental variability and habitat complexity in shallow ponds could provide refuges that reduce predation efficiency and weaken the relationship between macroinvertebrate and zooplankton body size. Altogether, these factors may explain why macroinvertebrate predation appeared to play a weaker or more context-dependent role in zooplankton body size than fish predation.

In the case of copepods, in addition to temperature/latitude and fish predation, pond morphometry

also had a significant effect on body size metrics, with both mean and maximum body size generally increasing with pond area. This pattern may be explained by greater habitat complexity and microhabitat availability in larger ponds (Compte et al., 2016; Karpowicz et al., 2019; Goździewicz et al., 2021), which could support the persistence of larger individuals. For instance, extensive shallow areas in ponds often include higher macrophyte coverage, potentially offering refuge for copepods and reducing predation risk (Sagrario et al., 2009). Moreover, we cannot rule out an indirect effect of pond area on resource availability (Schoener, 1989). In contrast, pond morphometry did not have significant effects on cladocerans body size metrics, suggesting that their body size structure is less influenced by habitat morphology and more strongly constrained by other ecological drivers, such as predation pressure or temperature. These differences highlight the distinct ways copepods and cladocerans interact with pond habitats and underscore the importance of taxon-specific responses when assessing patterns of body size variation. Copepods often exhibit longer generation times, more complex life cycles, and a stronger dependence on habitat stability (Allan, 1976; Sommer & Sommer, 2006). Larger and deeper ponds usually provide more stable physical conditions (e.g., less drying, more thermal buffering), which can favor the persistence of larger-bodied copepod species or allow individuals to grow larger (Skjoldal & Aarflot, 2023). In contrast, cladocerans typically reproduce rapidly and can colonize temporary or small ponds more easily, making them less dependent on pond morphology (Sommer & Sommer, 2006; Stenert et al., 2017). This difference may reflect fundamental ecological and life-history differences, with copepods being more sensitive to habitat stability and spatial structure, both of which increase with pond size, and their community composition often shifting toward larger-bodied taxa in larger ponds (Sommer & Sommer, 2006; Skjoldal & Aarflot, 2023). In contrast, cladocerans are rapid colonizers with broad tolerances, and their body size appears to be more strongly shaped by top-down drivers than by bottom-up or habitat-related factors (Skjoldal & Aarflot, 2023).

Additionally, our analyses revealed that the *pond* itself had a significant influence on maximum body size variation, independent of the measured factors such as temperature, predation, or pond area. This

pond effect suggests that the repeated sampling in certain ponds could indicate the presence of spatial autocorrelation, as well as the influence of unmeasured local conditions, such as microhabitat structure, localized predator or prey assemblages, water chemistry, land-use or other pond-specific ecological contexts play an important role in shaping crustacean body size (Galindo et al., 1994; Bruçet et al., 2005; Meerhoff et al., 2007b; Kagalou et al., 2010). In other words, even after accounting for broad environmental gradients and key biological drivers, a substantial portion of size variation remains tied to individual pond characteristics. This highlights the importance of local heterogeneity and context-dependent effects, emphasizing that ecological patterns observed at the regional scale may be strongly modulated by site-specific factors.

Altogether, our results underscore the combined influence of multiple factors in shaping crustacean body size in pond ecosystems. Nevertheless, in contrast to previous studies that highlighted the role of food resource availability in influencing crustaceans' size (Jeppesen et al., 2000; Lefort et al., 2015), in the present study, bottom-up control exerted by resource availability (i.e., chlorophyll-a concentration) did not emerge as a significant predictor of crustacean body size in ponds. As a result, we reject our third hypothesis which proposed that body size would increase with greater food availability, under the assumption that abundant resources promote the growth of larger individuals. It is worth mentioning that, in the studied ponds, chlorophyll-a may have been a limited indicator of food availability for crustaceans, as many feed on heterotrophic organisms such as ciliates and flagellates (Allan, 1976; Burns & Schallenberg, 2001; Kiørboe, 2011), which lack this pigment. Consequently, crustaceans may be less sensitive to changes in chlorophyll-a concentration alone.

Although our study spans two continents and covers a wide latitudinal gradient, it is important to acknowledge that our sampling effort did not include tropical regions (between  $-30^{\circ}$  and  $30^{\circ}$  latitude). This geographic gap limits the extent to which our findings can be generalized to lower latitudes, where environmental conditions and ecological interactions may differ substantially from those in temperate regions. For instance, higher and more stable annual temperatures, distinct predator communities with higher predation pressure, and continuous primary

production in tropical ponds could modulate crustacean body size patterns in ways not captured by our dataset. Therefore, while our results highlight temperature and predation pressure as key drivers of cladoceran and copepod body sizes across temperate and subtropical ponds, further research is needed to assess whether these patterns hold in tropical systems. Addressing this gap will be essential to build a more comprehensive understanding of the global determinants of zooplankton body size. From a biogeographical perspective, it would also be valuable to incorporate ponds located at different elevations to explore how altitude interacts with latitude in shaping crustacean body size. On the other hand, future work should consider broader assessments of crustacean diets, moving beyond proxies such as chlorophyll-a, which capture only autotrophic organisms, and do not account for heterotrophic prey such as ciliates and flagellates that are important, especially for omnivorous taxa. Finally, given the strong influence of fish predation on crustacean body size in ponds, identifying whether certain fish species or abundances exert stronger predation pressure would further clarify the role of top-down control in shaping crustacean body size.

Building on these considerations, it is also important to recognize that temperature effects on crustacean body size may vary among taxa and be influenced by species composition. Taxon-specific responses have been observed in crustacean zooplankton; for example, Havens et al. (2015) reported a more pronounced decline in body size in cyclopoid copepods with increasing temperature, whereas calanoid copepods showed no significant effect, highlighting the complexity of temperature effects across different copepod groups. Unlike these taxon-specific approaches, our study focuses on broader functional groups, which may limit the detection of within-group responses. Moreover, temperature differences in body size may not only result from the effect of temperature on body size within a species, but may also be shaped by species turnover or shifts in community composition (Brandão et al., 2021). Consequently, while our results capture general trends in copepod and cladoceran body size in relation to temperature, they do not allow us to determine species-specific responses or disentangle the effects of community composition, which remain important avenues for future research.

The findings of this study have important implications in the context of climate change, as ponds are especially sensitive to climate variability, and air temperature and latitudinal gradients can serve as natural proxies for future warming scenarios. The consistent pattern of decreasing crustacean body size toward higher temperatures and lower latitudes suggests that ongoing climate warming could drive similar shifts in body size distributions across regions. As global temperatures continue to rise, pond ecosystems at higher latitudes may begin to resemble those currently found in the lower latitudes or in higher temperatures, with smaller-bodied size dominating aquatic communities in ponds. This reduction in body size in crustaceans may alter key ecosystem processes, including energy transfer efficiency to higher trophic levels, nutrient recycling rates, and the likelihood of regime shifts (i.e., clear-water versus turbid-water). Crucially, the robustness of these patterns is supported by the consistency of results across models using different geographic and climatic predictors considering countries in both hemispheres. In all cases, body size increased toward lower temperatures and decreased in the presence of predators such as fish, highlighting the joint influence of abiotic gradients and biotic pressures. Furthermore, the positive relationship between pond area and body size in copepods suggests that habitat loss may disproportionately impact larger copepods individuals, potentially declining the size structure of aquatic communities. Overall, these results underscore the vulnerability of pond ecosystems to climate change and emphasize the importance of considering both abiotic and biotic drivers of size structure when predicting the ecological consequences of climate change on ponds' food webs.

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**Data availability** The datasets used in this study are available upon reasonable request.

#### Declarations

**Competing interest** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Ethics approval** No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

**Consent to participate** All authors declare that there is no conflict in participating in this study and have given their full consent.

**Consent to publish** All authors agree to the publication of this manuscript and declare no conflict regarding publishing.

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## References

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723. <https://doi.org/10.1109/TAC.1974.1100705>.
- Albini, D., E. Ransome, A. Dumbrell, S. Pawar, E. O’Gorman, T. Smith, T. Bell, M. Jackson & G. Woodward, 2025. Warming alters plankton body-size distributions in a large field experiment. *Communications Biology*. <https://doi.org/10.1038/s42003-024-07380-2>.
- Allan, J. D., 1976. Life history patterns in zooplankton. university of chicago press. *The American Naturalist* 110: 165–180. <https://doi.org/10.1086/283056>.
- Aranguren-Riano, N., C. Guisande & R. Ospina, 2011. Factors controlling crustacean zooplankton species richness in Neotropical lakes. *Journal of Plankton Research* 33: 1295–1303. <https://doi.org/10.1093/plankt/fbr028>.
- Atkinson, D., 1994. Temperature and Organism Size—A Biological Law for Ectotherms? In Begon, M. & A. H. Fitter (eds), *Advances in Ecological Research Academic Press*: 1–58.
- Bartón, K., 2023. MuMin: Multi-Model Inference. URL <https://cran.r-project.org/web/packages/MuMin/index.html>.
- Bartrons, M., J. Yang, M. Cuenca-Cambronero, P. Lemmens, M. Anton-Pardo, M. Beklioglu, J. Biggs, A. Boissezon, D. Boix, C. Calvo, M. Colina, T. A. Davidson, L. De Meester, J. C. Fahy, H. M. Greaves, H. Kiran Isufi, E. E. Levi, M. Meerhoff, T. Mehner, E. B. Mülâyim, B. Oertli, I. R. Patmore, C. D. Sayer, J. Villà-Freixa & S. Brucet, 2025. Why ponds concentrate nutrients: the roles of internal features, land use, and climate. *Hydrobiologia*. <https://doi.org/10.1007/s10750-025-05907-0>.
- Bates, D., M. Mächler, B. Bolker & S. Walker, 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. 67: 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Benke, A. C., A. D. Huryn, L. A. Smock & J. B. Wallace, 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the Southeastern United States. *Journal of the North American Benthological Society* 18: 308–343. <https://doi.org/10.2307/1468447>.
- Brandão, M. C., F. Benedetti, S. Martini, Y. D. Soviadan, J.-O. Irissou, J.-B. Romagnan, A. Elineau, C. Desnos, L. Jalabert, A. S. Freire, M. Picheral, L. Guidi, G. Gorsky, C. Bowler, L. Karp-Boss, N. Henry, C. de Vargas, M. B. Sullivan, L. Stemann & F. Lombard, 2021. Macroscale patterns of oceanic zooplankton composition and size structure. *Nature Publishing Group. Scientific Reports* 11: 15714. <https://doi.org/10.1038/s41598-021-94615-5>.
- Brooks, J. L. & S. I. Dodson, 1965. Predation, body size, and composition of plankton. *American association for the advancement of science. Science* 150: 28–35. <https://doi.org/10.1126/science.150.3692.28>.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage & G. B. West, 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789. <https://doi.org/10.1890/03-9000>.
- Brown, J. H., A. P. Allen & J. F. Gillooly, 2007. The metabolic theory of ecology and the role of body size in marine and freshwater ecosystems. In Hildrew, A. G., D. G. Raffaelli & R. Edmonds-Brown (eds), *Body Size: The Structure and Function of Aquatic Ecosystems Cambridge University Press*: 1–15.
- Brucet, S., D.L.-F. Boix, R. Moreno-Amich & X. D. Quintana, 2005. Zooplankton structure and dynamics in permanent and temporary Mediterranean salt marshes: taxon-based and size-based approaches. *Archiv Für Hydrobiologie* 162: 535–555. <https://doi.org/10.1127/0003-9136/2005/0162-0535>.
- Brucet, S., D. Boix, X. D. Quintana, E. Jensen, L. W. Nathansen, C. Trochine, M. Meerhoff, S. Gascón & E. Jeppesena, 2010. Factors influencing zooplankton size structure at contrasting temperatures in coastal shallow lakes: Implications for effects of climate change. *Limnology and Oceanography* 55: 1697–1711. <https://doi.org/10.4319/lo.2010.55.4.1697>.
- Brys, R., D. Halfmaerten, & S. Neyrinck, 2021. eDNA sampling guide for lentic waters. *Research Institute for Nature and Forest* : 16.
- Burns, C. W. & M. Schallenberg, 2001. Calanoid copepods versus cladocerans: consumer effects on protozoa in lakes of different trophic status. *Limnology and Oceanography* 46: 1558–1565. <https://doi.org/10.4319/lo.2001.46.6.1558>.
- Burton, T. & S. Einum, 2020. The old and the large may suffer disproportionately during episodes of high temperature: evidence from a keystone zooplankton species. *Conservation Physiology* 8: Coaa038. <https://doi.org/10.1093/conphys/coaa038>.
- Cérégino, R., D. Boix, H.-M. Cauchie, K. Martens & B. Oertli, 2014. The ecological role of ponds in a changing world. *Hydrobiologia* 723: 1–6. <https://doi.org/10.1007/s10750-013-1719-y>.
- Coghlan, A. R., J. L. Blanchard, S. Wotherspoon, R. D. Stuart-Smith, G. J. Edgar, N. Barrett & A. Audzijonyte, 2024. Mean reef fish body size decreases towards warmer waters. *Ecology Letters* 27: e14375. <https://doi.org/10.1111/ele.14375>.
- Compte, J., M. Montenegro, A. Ruhí, S. Gascón, J. Sala & D. Boix, 2016. Microhabitat selection and diel patterns of zooplankton in a Mediterranean temporary pond. *Hydrobiologia* 766: 201–213. <https://doi.org/10.1007/s10750-015-2455-2>.
- Cuenca-Cambronero, M., M. Blicharska, J.-A. Perrin, T. A. Davidson, B. Oertli, M. Lago, M. Beklioglu, M. Meerhoff, M. Arim, J. Teixeira, L. De Meester, J. Biggs, J. Robin, B. Martin, H. M. Greaves, C. D. Sayer, P. Lemmens, D. Boix, T. Mehner, M. Bartrons & S. Brucet, 2023. Challenges and opportunities in the use of ponds and ponds as nature-based solutions. *Hydrobiologia* 850: 3257–3271. <https://doi.org/10.1007/s10750-023-05149-y>.
- das Candeias, D. A., D. A. Moi, N. R. Simões, F. Azevedo, M. Meerhoff & C. C. Bonecker, 2022. High temperature, predation, nutrient, and food quality drive dominance of small-sized zooplankton in Neotropical lakes. *Aquatic Sciences*. <https://doi.org/10.1007/s00027-022-00881-4>.
- Daufresne, M., K. Lengfellner & U. Sommer, 2009. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the*

- United States of America 106: 12788–12793. <https://doi.org/10.1073/pnas.0902080106>.
- Deutsch, C., J. L. Penn, W. C. E. P. Verberk, K. Inomura, M.-G. Endress & J. L. Payne, 2022. Impact of warming on aquatic body sizes explained by metabolic scaling from microbes to macrofauna. *Proceedings of the National Academy of Sciences*. 119: e2201345119. <https://doi.org/10.1073/pnas.2201345119>.
- Emmrich, M., S. Pédrón, S. Brucet, I. J. Winfield, E. Jeppesen, P. Volta, C. Argillier, T. L. Lauridsen, K. Holmgren, T. Hesthagen & T. Mehner, 2014. Geographical patterns in the body-size structure of European lake fish assemblages along abiotic and biotic gradients. *Journal of Biogeography* 41: 2221–2233. <https://doi.org/10.1111/jbi.12366>.
- Escribano, R., E. Bustos-Ríos, P. Hidalgo & C. E. Morales, 2016. Non-limiting food conditions for growth and production of the copepod community in a highly productive upwelling zone. *Continental Shelf Research* 126: 1–14. <https://doi.org/10.1016/j.csr.2016.07.018>.
- Evans, L. E., A. G. Hirst, P. Kratina & G. Beaugrand, 2020. Temperature-mediated changes in zooplankton body size: large scale temporal and spatial analysis. *Ecography* 43: 581–590. <https://doi.org/10.1111/ecog.04631>.
- Fluet-Chouinard, E., B. D. Stocker, Z. Zhang, A. Malhotra, J. R. Melton, B. Poulter, J. O. Kaplan, K. K. Goldewijk, S. Siebert, T. Minayeva, G. Hugelius, H. Joosten, A. Barthelmes, C. Prigent, F. Aires, A. M. Hoyt, N. Davidson, C. M. Finlayson, B. Lehner, R. B. Jackson & P. B. McIntyre, 2023. Extensive global wetland loss over the past three centuries. *Nature* 614: 281–286. <https://doi.org/10.1038/s41586-022-05572-6>.
- Forster, J., A. G. Hirst & D. Atkinson, 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences*. 109(47): 19310–19314. <https://doi.org/10.1073/pnas.1210460109>.
- Fox, J., S. Weisberg, & B. Price, 2001. car: Companion to Applied Regression. , 3.1–3.
- Galindo, M. D., A. J. Mata, N. Mazuelos & L. Serrano, 1994. Microcrustacean and rotifer diversity and richness relating to water temporality in dune ponds of the Doñana National Park (SW Spain). *Taylor & Francis. SIL Proceedings 1922–2010(25)*: 1350–1356. <https://doi.org/10.1080/03680770.1992.11900392>.
- Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph & R. Heinsohn, 2011. Declining body size: a third universal response to warming? *Trends in Ecology & Evolution* 26: 285–291. <https://doi.org/10.1016/j.tree.2011.03.005>.
- Gillooly, J. F., 2000. Effect of body size and temperature on generation time in zooplankton. *Journal of Plankton Research* 22: 241–251. <https://doi.org/10.1093/plankt/22.2.241>.
- Gillooly, J. F. & S. I. Dodson, 2000. Latitudinal patterns in the size distribution and seasonal dynamics of new world, freshwater cladocerans. *Limnology and Oceanography* 45: 22–30. <https://doi.org/10.4319/lo.2000.45.1.0022>.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage & E. L. Charnov, 2001. Effects of size and temperature on metabolic rate. *Science (New York, N.y.)* 293: 2248–2251. <https://doi.org/10.1126/science.1061967>.
- Goździewicz, A. M., J. Koszałka, R. Tandyrak, J. Grochowska & K. Parszuto, 2021. Functional responses of zooplankton communities to depth, trophic status, and ion content in mine pit lakes. *Hydrobiologia* 848: 2699–2719. <https://doi.org/10.1007/s10750-021-04590-1>.
- Gyllström, M., L.-A. Hansson, E. Jeppesen, F. G. Criado, E. Gross, K. Irvine, T. Kairesalo, R. Kornijow, M. R. Miracle, M. Nykänen, T. Nöges, S. Romo, D. Stephen, E. V. Donk & B. Moss, 2005. The role of climate in shaping zooplankton communities of shallow lakes. *Limnology and Oceanography* 50: 2008–2021. <https://doi.org/10.4319/lo.2005.50.6.2008>.
- Hansen, M. J. & D. H. Wahl, 1981. Selection of small daphnia pulex by yellow perch fry in oneida lake, New York. *Transactions of the American Fisheries Society* 110: 64–71. [https://doi.org/10.1577/1548-8659\(1981\)110%3c64:SOSDPB%3e2.0.CO;2](https://doi.org/10.1577/1548-8659(1981)110%3c64:SOSDPB%3e2.0.CO;2).
- Havens, K. E., R. M. Pinto-Coelho, M. Bekliöglü, K. S. Christoffersen, E. Jeppesen, T. L. Lauridsen, A. Mazumder, G. Méthot, B. P. Alloul, U. N. Tavşanoğlu, Ş Erdoğan & J. Vijverberg, 2015. Temperature effects on body size of freshwater crustacean zooplankton from Greenland to the tropics. *Hydrobiologia* 743: 27–35. <https://doi.org/10.1007/s10750-014-2000-8>.
- Herwig, B. R. & D. E. Schindler, 1996. Effects of aquatic insect predators on zooplankton in fishless ponds. *Hydrobiologia* 324: 141–147. <https://doi.org/10.1007/BF00018175>.
- Hildrew, A. G., D. G. Raffaelli & R. Edmonds-Brown, 2007. *Body Size: The Structure and Function of Aquatic Ecosystems*, Cambridge University Press, Cambridge.
- Hill, M. J., H. M. Greaves, C. D. Sayer, C. Hassall, M. Milin, V. S. Milner, L. Marazzi, R. Hall, L. R. Harper, I. Thornhill, R. Walton, J. Biggs, N. Ewald, A. Law, N. Willby, J. C. White, R. A. Briers, K. L. Mathers, M. J. Jeffries & P. J. Wood, 2021. Pond ecology and conservation: research priorities and knowledge gaps. *Ecosphere* 12: e03853. <https://doi.org/10.1002/ecs2.3853>.
- Horne, C. R., A. G. Hirst & D. Atkinson, 2015. Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. *Ecology Letters* 18: 327–335. <https://doi.org/10.1111/ele.12413>.
- Horne, C. R., A. G. Hirst, D. Atkinson, A. Neves & T. Kjørboe, 2016. A global synthesis of seasonal temperature-size responses in copepods. *Global Ecology and Biogeography* 25: 988–999. <https://doi.org/10.1111/geb.12460>.
- Iglesias, C., N. Mazzeo, M. Meerhoff, G. Lacerot, J. M. Clemente, F. Scasso, C. Kruk, G. Goyenola, J. García-Alonso, S. L. Amsinck, J. C. Paggi, S. José de Paggi & E. Jeppesen, 2011. High predation is of key importance for dominance of small-bodied zooplankton in warm shallow lakes: evidence from lakes, fish enclosures and surface sediments. *Hydrobiologia* 667: 133–147. <https://doi.org/10.1007/s10750-011-0645-0>.
- Jeppesen, E., J. Peder Jensen, M. SØndergaard, T. Lauridsen & F. Landkildehus, 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biology* 45: 201–218. <https://doi.org/10.1046/j.1365-2427.2000.00675.x>.

- Jr, F. E. H., 2025. Hmisc: Harrell Miscellaneous.
- Kagalou, I. I., A. Kosiori & I. D. Leonardos, 2010. Assessing the zooplankton community and environmental factors in a Mediterranean wetland. *Environmental Monitoring and Assessment* 170: 445–455. <https://doi.org/10.1007/s10661-009-1245-6>.
- Karpowicz, M., J. Ejsmont-Karabin, A. Więcko, G. Andrzej & A. Cudowski, 2019. A place in space - the horizontal vs vertical factors that influence zooplankton (Rotifera, Crustacea) communities in a mesotrophic lake. *Journal of Limnology*. <https://doi.org/10.4081/jlimnol.2019.1886>.
- Kjørboe, T., 2008. A mechanistic approach to plankton ecology. Princeton University Press, Princeton.
- Kjørboe, T., 2011. How zooplankton feed: mechanisms, traits and trade-offs. *Biological Reviews* 86: 311–339. <https://doi.org/10.1111/j.1469-185X.2010.00148.x>.
- Kratina, P., H. S. Greig, P. L. Thompson, T. S. A. Carvalho-Pereira & J. B. Shurin, 2012. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology* 93: 1421–1430. <https://doi.org/10.1890/11-1595.1>.
- Lefort, S., O. Aumont, L. Bopp, T. Arsouze, M. Gehlen & O. Maury, 2015. Spatial and body-size dependent response of marine pelagic communities to projected global climate change. *Global Change Biology* 21: 154–164. <https://doi.org/10.1111/gcb.12679>.
- Li, H., Y. Gu, Q. Cai, X. Dong, & L. Ye, 2022. Zooplankton Size Structure in Relation to Environmental Factors in the Xiangxi Bay of Three Gorges Reservoir, China. *Frontiers in Ecology and Evolution* 10
- Litchman, E., M. D. Ohman & T. Kjørboe, 2013. Trait-based approaches to zooplankton communities. *Journal of Plankton Research* 35: 473–484. <https://doi.org/10.1093/plankt/fbt019>.
- López-de Sancha, A., L. Benejam, D. Boix, L. Briggs, M. Cuenca-Cambronero, T. A. Davidson, L. De Meester, J. C. Fahy, P. Lemmens, B. Martin, T. Mehner, B. Oertli, M. Rasmussen, H. M. Greaves, C. Sayer, M. Beklioglu, R. Brys & S. Brucet, 2025a. Drivers of amphibian species richness in European ponds. *Ecography*. <https://doi.org/10.1111/ecog.07347>.
- López-de Sancha, A., D. Boix, L. Benejam, L. Briggs, T. A. Davidson, J. C. Fahy, V. Frutos-Aragón, H. M. Greaves, P. Lemmens, T. Mehner, L. Martín, B. Oertli, C. Sayer & S. Brucet, 2025b. Amphibian conservation in Europe: the importance of pond condition. *Biodiversity and Conservation*. <https://doi.org/10.1007/s10531-025-03033-w>.
- Lüdecke, D., 2018. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *Journal of Open Source Software*. <https://doi.org/10.21105/joss.00772>.
- Meerhoff, M., J. M. Clemente, F. T. De Mello, C. Iglesias, A. R. Pedersen & E. Jeppesen, 2007a. Can warm climate-related structure of littoral predator assemblies weaken the clear water state in shallow lakes? *Global Change Biology* 13: 1888–1897. <https://doi.org/10.1111/j.1365-2486.2007.01408.x>.
- Meerhoff, M., C. Iglesias, F. T. De Mello, J. M. Clemente, E. Jensen, T. L. Lauridsen & E. Jeppesen, 2007b. Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshwater Biology* 52: 1009–1021. <https://doi.org/10.1111/j.1365-2427.2007.01748.x>.
- Moore, M., C. L. Folt & R. Stemberger, 1996. Consequences of elevated temperatures for zooplankton assemblages in temperate lakes. *Archiv fur Hydrobiologie*. <https://doi.org/10.1127/archiv-hydrobiol/135/1996/289>.
- Oertli, B., D. A. Joye, E. Castella, R. Juge, D. Cambin & J.-B. Lachavanne, 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation* 104: 59–70. [https://doi.org/10.1016/S0006-3207\(01\)00154-9](https://doi.org/10.1016/S0006-3207(01)00154-9).
- Oertli, B., J. Biggs, R. Céréghino, P. Grillas, P. Joly & J.-B. Lachavanne, 2005. Conservation and monitoring of pond biodiversity: introduction. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15: 535–540. <https://doi.org/10.1002/aqc.752>.
- Ohlberger, J., 2013. Climate warming and ectotherm body size – from individual physiology to community ecology. *Functional Ecology* 27: 991–1001. <https://doi.org/10.1111/1365-2435.12098>.
- Peterson, R. A., 2021. Finding Optimal Normalizing Transformations via bestNormalize. *The R Journal* 13: 294–313.
- Peterson, B. G., P. Carl, K. Boudt, R. Bennett, J. Ulrich, E. Zivot, D. Cornilly, E. Hung, M. Lestel, K. Balkissoon, D. Wuertz, A. A. Christidis, R. D. Martin, Z. Z. Zhou, J. M. Shea, & D. Jain, 2024. PerformanceAnalytics: Econometric Tools for Performance and Risk Analysis.
- Rincón-Palau, K., A. Badosa, M. Cuenca-Cambronero, C. Trochine, S. Sgarzi, X. D. Quintana, D. Boix & S. Brucet, 2025. The Size Structure of the Zooplankton Community Reflects Better the Trophic Status of Mediterranean Ponds Than the Taxonomic Structure. *Freshwater Biology* 70: e70101. <https://doi.org/10.1111/fwb.70101>.
- Sagrario, G., M. De Los Angeles, E. Balseiro, R. Ituarte & E. Spivak, 2009. Macrophytes as refuge or risky area for zooplankton: a balance set by littoral predacious macroinvertebrates. *Freshwater Biology* 54: 1042–1053. <https://doi.org/10.1111/j.1365-2427.2008.02152.x>.
- Saito, V. S., D. M. Perkins & P. Kratina, 2021. A metabolic perspective of stochastic community assembly. *Trends in Ecology & Evolution* 36: 280–283. <https://doi.org/10.1016/j.tree.2021.01.003>.
- Schoener, T. W., 1989. Food webs from the small to the large: the Robert H. Macarthur award lecture. *Ecological Society of America. Ecology* 70: 1559–1589. <https://doi.org/10.2307/1938088>.
- Segovia, B. T., D. G. Pereira, L. M. Bini, B. R. De Meira, V. S. Nishida, F. A. Lansac-Tôha & L. F. M. Velho, 2015. The role of microorganisms in a planktonic food web of a floodplain lake. *Microbial Ecology* 69: 225–233. <https://doi.org/10.1007/s00248-014-0486-2>.
- Shurin, J. B., 2001. Interactive effects of predation and dispersal on zooplankton communities. *Ecology* 82: 3404–3416. [https://doi.org/10.1890/0012-9658\(2001\)082\[3404:IEO-PAD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[3404:IEO-PAD]2.0.CO;2).
- Shurin, J. B., D. S. Gruner & H. Hillebrand, 2005. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Royal Society. Proceedings of the Royal Society b: Biological Sciences* 273: 1–9. <https://doi.org/10.1098/rspb.2005.3377>.

- Shurin, J. B., J. L. Clasen, H. S. Greig, P. Kratina & P. L. Thompson, 2012. Warming shifts top-down and bottom-up control of pond food web structure and function. *Philosophical Transactions of the Royal Society b: Biological Sciences* 367: 3008–3017. <https://doi.org/10.1098/rstb.2012.0243>.
- Skjoldal, H. R. & J. M. Aarflot, 2023. Abundance and biomass of copepods and cladocerans in Atlantic and Arctic domains of the Barents Sea ecosystem. *Journal of Plankton Research* 45: 870–884. <https://doi.org/10.1093/plankt/fbad043>.
- Sommer, U. & F. Sommer, 2006. Cladocerans versus copepods: the cause of contrasting top-down controls on freshwater and marine phytoplankton. *Oecologia* 147: 183–194. <https://doi.org/10.1007/s00442-005-0320-0>.
- Stenert, C., R. Wüsth, M. M. Pires, R. F. Freiry, D. Nielsen & L. Maltchik, 2017. Composition of cladoceran dormant stages in intermittent ponds with different hydroperiod lengths. *Ecological Research* 32: 921–930. <https://doi.org/10.1007/s11284-017-1498-4>.
- Suchy, K. D., K. Young, M. Galbraith, R. I. Perry & M. Costa, 2022. Match/Mismatch Between Phytoplankton and Crustacean Zooplankton Phenology in the Strait of Georgia, *Frontiers in Marine Science*, Canada: <https://doi.org/10.3389/fmars.2022.832684>.
- Taiyun, 2025. taiyun/corrplot.
- Wang, L., X. Ma & J. Chen, 2023. Do submerged macrophyte species influence crustacean zooplankton functional group richness and their resource use efficiency in the low-light environment?, *Frontiers in Plant Science*, *Frontiers*: <https://doi.org/10.3389/fpls.2023.1185947>.
- White, E. P., S. K. M. Ernest, A. J. Kerkhoff & B. J. Enquist, 2007. Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution* 22: 323–330. <https://doi.org/10.1016/j.tree.2007.03.007>.
- Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. URL <https://cran.r-project.org/web/packages/ggplot2/citation.html>.
- Williams, P., M. Whitfield, J. Biggs, S. Bray, G. Fox, P. Nicolet & D. Sear, 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation* 115: 329–341. [https://doi.org/10.1016/S0006-3207\(03\)00153-8](https://doi.org/10.1016/S0006-3207(03)00153-8).
- Wong, B. & F. J. Ward, 1972. Size selection of daphnia pulex by yellow perch (perca flavescens) fry in west blue lake, manitoba. nrc research press. *Journal of the Fisheries Research Board of Canada* 29: 1761–1764. <https://doi.org/10.1139/f72-277>.
- Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido & P. H. Warren, 2005. Body size in ecological networks. *Trends in Ecology & Evolution* 20: 402–409. <https://doi.org/10.1016/j.tree.2005.04.005>.
- Woodward, G., D. M. Perkins & L. E. Brown, 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society b: Biological Sciences* 365: 2093–2106. <https://doi.org/10.1098/rstb.2010.0055>.
- Woolway, R. I., S. Sharma & J. P. Smol, 2022. Lakes in hot water: the impacts of a changing climate on aquatic ecosystems. *BioScience* 72: 1050–1061. <https://doi.org/10.1093/biosci/biac052>.
- Yvon-Durocher, G., J. M. Montoya, M. Trimmer & G. Woodward, 2011. Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Global Change Biology* 17: 1681–1694. <https://doi.org/10.1111/j.1365-2486.2010.02321.x>.
- Zeileis, A., & T. Hothorn, 2002. Diagnostic Checking in Regression Relationships.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev & G. M. Smith, 2009. Mixed effects models and extensions in ecology with R, Springer, New York, New York, NY:

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