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RESEARCH ARTICLE

Long-term changes in intra- and interspecific trait variability of a small herbivore in a deep perialpine lake

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Abstract

Analyses of trait dynamics provide new insights into the dynamics of communities and ecosystems. While zooplankton traits—and especially the defensive traits—of zooplankton are well studied in the laboratory, there are hardly any studies analyzing long-term dynamics of zooplankton traits. Here, we study species turnover and trait dynamics of three species of the genus *Bosmina*, *Bosmina coregoni*, *Bosmina longispina*, and *Bosmina longirostris*, at the genus and species levels during three decades of environmental changes in Lake Constance. We showed that *Bosmina* species turnover substantially influenced genus-level body size distributions and key defensive traits, including mucro and antennule sizes. Results also showed that mean species traits more effectively predicted genus-level traits when interspecies trait differences were large, making them particularly reliable in species-rich contexts. In contrast, when trait differences among species were small, intraspecific variations may obscure genus-level temporal patterns. In addition, we found within-species trait changes that partially paralleled those observed at the genus level, but also within-species trait changes that partially differed from those observed at the genus level. While a large reduction of nutrients during two decades appeared not to be strongly associated with changes in *Bosmina* species composition and trait dynamics, large and rapid species turnover and trait changes coincided with 7 yr of increased stickleback densities in the pelagic zone of the lake.

In the realm of ecology, there is a growing trend toward emphasizing the analysis of traits rather than exclusively focusing on species composition. This shift is often characterized as the "biodiversity revolution" (Cernansky 2017). The rationale behind this approach lies in the utility of traits as a pivotal tool for elucidating and generalizing mechanisms governing the assembly of biodiversity. Furthermore, analyses of trait dynamics facilitate a deeper understanding of ecological and physiological processes (McGill et al. 2006; Shipley et al. 2006) and enable predictions regarding the impact of species and communities on ecosystem functions and services (Greenwell et al. 2019; Schibalski et al. 2022).

Traits encompass a broad spectrum of characteristics, including morphological, physiological, phenological, cultural, and behavioral attributes, and they are quantifiable across various scales, ranging from individual organisms to genetic, species, population, and community levels (McGill et al. 2006; Violle et al. 2007). Functional traits exert an indirect influence on an organism's fitness by affecting processes such as growth, reproduction, and survival (Violle et al. 2007). Key traits are those that prominently characterize an organism's fitness (Litchman et al. 2013). Functional traits, in particular, play a pivotal role in defining the ecological roles of species, delineating how they interact with their environment and other species (Díaz and Cabido 2001). Numerous studies have emphasized the pivotal role of species' functional traits in governing ecosystem functioning (Chen et al. 2023). In particular, community-level functional traits have been shown to better elucidate variations in ecosystem functioning compared to species-based matrices (Roscher et al. 2012). Functional trait-based approaches are increasingly used to understand ecological dynamics across levels of organization, from populations to entire ecosystems (Kremer et al. 2017; Martini et al. 2021).

A prevalent method for examining trait–environment relationships is through the calculation of community-weighted mean (CWM) trait values, which summarize the average trait

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expression in a community weighted by species' relative abundances (Lavorel and Garnier 2002; Ricotta and Moretti 2011). In aquatic ecosystems, trait-based analyses have been effectively applied to various communities, including phytoplankton (Fragoso et al. 2019; Zhang et al. 2024), macrozoobenthos (Bosco Gusmao et al. 2022), and zooplankton assemblages (Obertegger and Flaim 2015; Brun et al. 2016). Spatial differences or temporal changes in CWM values can be influenced by species turnover when species differ in their trait values. Additionally, intraspecific variation—driven by processes such as phenotypic plasticity or evolutionary adaptation—can also influence these changes (Schaffner et al. 2019; Isanta-Navarro et al. 2021; Gallego and Narwani 2022). However, many studies, particularly those focusing on plankton communities, typically rely on mean trait values assigned to species, often derived from laboratory measurements (Edwards et al. 2013; Pranger et al. 2025). Obviously, such an approach does not allow for the study of the relative importance of species turnover vs. within-species trait changes for CWM traits. Moreover, it prevents the evaluation of whether within-species trait changes enhance or mask the effects of species turnover. There is a notable gap in the literature—especially for plankton systems—regarding studies that analyze the importance of intraspecific trait variability in shaping trait patterns at higher levels of taxonomical or ecological aggregation.

Members of the genus *Bosmina* are ubiquitous and abundant small herbivores in lake ecosystems. *Bosmina* species have been extensively studied regarding cyclomorphosis (Black and Hairston 1983; Chang and Hanazato 2003), predator-induced defenses (Chang and Hanazato 2004; McNaught and Weber 2009; Kerfoot and Savage 2016), and as indicators of ecosystem change, primarily due to their well-preserved remains in lake sediments (Korosi et al. 2013). In many lakes, multiple *Bosmina* species or morphotypes coexist, exhibiting differences in antennule size and shape, as well as the presence and size of mucro, a small posterior spine on the carapace that functions as a defensive structure. Variations in these morphological traits have been shown to be induced by invertebrate predators. Additionally, fish predation may influence *Bosmina* eye size through visibility selection (Zaret and Kerfoot 1975), while food availability strongly affects reproductive traits such as clutch sizes and maturation sizes (Kerfoot 1974; Goulden et al. 1982; Branstrator and Lehman 1991). Therefore, *Bosmina* serves as an ideal case study to investigate trait dynamics at both the genus and species levels.

In this study, we examined the morphological and life history traits of *Bosmina* spp. over three decades of oligotrophication and changes in fish predation pressure. We analyzed how *Bosmina* traits at the species and genus level responded to environmental changes. Subsequently, we assessed whether genus-level trait dynamics are mainly driven by shifts in relative frequencies of *Bosmina* species or by changes within species, and to which extent genus trait dynamics are enhanced or dampened by within-species dynamics.

Materials and methods

Study site

Starting in the 1950s, Lake Constance (Fig. 1a), situated on the northern fringes of the European Alps, underwent eutrophication characterized by a surge in phosphorus concentration due to human activities (Güde et al. 1998). Subsequent extensive restoration initiatives, including the construction of wastewater treatment facilities and the prohibition of phosphorus in detergents, resulted in declined phosphorus levels. During 1987–2019, the period when preserved samples were available, total phosphorus concentrations during winter mixis declined from > 50 to $< 10\,\mu$g TP L^{-1} (Fig. 1b). This decline in phosphorus concentrations significantly influenced the phytoplankton (Jochimsen et al. 2013; Milan et al. 2022), zooplankton (Straile 2015), and fish community composition (Sabel et al. 2020). Lake-wide hydroacoustic scans of fish densities (since 2009) revealed that, from 2012 onwards, small fish densities were approximately 10-fold higher than during the initial sampling years (2009–2011) (Fig. 1c) (Eckmann and Engesser 2019), suggesting increased predation pressure on zooplankton (Ogorelec et al. 2022; Maier et al. 2023). This rise is strongly supported by long-term bycatch records (1991–2015), which showed no sticklebacks before 2012 but a sharp increase thereafter (Rösch et al. 2018: > 10% of nets in 2013–2014; > 20% of nets in 2015). Consistently, fish catches revealed that the majority (> 90%) of these small fish were sticklebacks (Alexander et al. 2016; Gugele et al. 2020). Abundances of *Bosmina* spp. declined in the first years of the study period (Straile and Müller 2010), but increased again in recent years (Fig. 1d).

Collection, processing, and identification of zooplankton

Zooplankton samples were collected from 140 to 0 m depth using a Clarke-Bumpus sampler with a mesh size of 140 μm on a weekly basis during the stratified period, and less frequently during winter months (Straile and Geller 1998; Straile 2015), in Überlinger See—a fjordlike, north-western extension of Upper Lake Constance (Fig. 1a). Geometric mean abundances of *Bosmina* spp. for the spring–summer season (April–August) were calculated from counts of these samples (Fig. 1d). Original counts did not distinguish between the different *Bosmina* species. Formalin-preserved samples dating back to 1987 are stored at the Limnological Institute, University of Konstanz, Germany, from which we chose one sample each from April, June, and August from 19 study years for analyses of *Bosmina* traits. The years (1987, 1989–1990, 1993, 1995, 1997–1998, 2000, 2003, 2005, 2008, 2010, 2012–2013, 2015–2019) were selected to ensure a maximum gap of 3 yr, with higher sampling frequency in the period following the stickleback increase (data available from 2009 onwards).

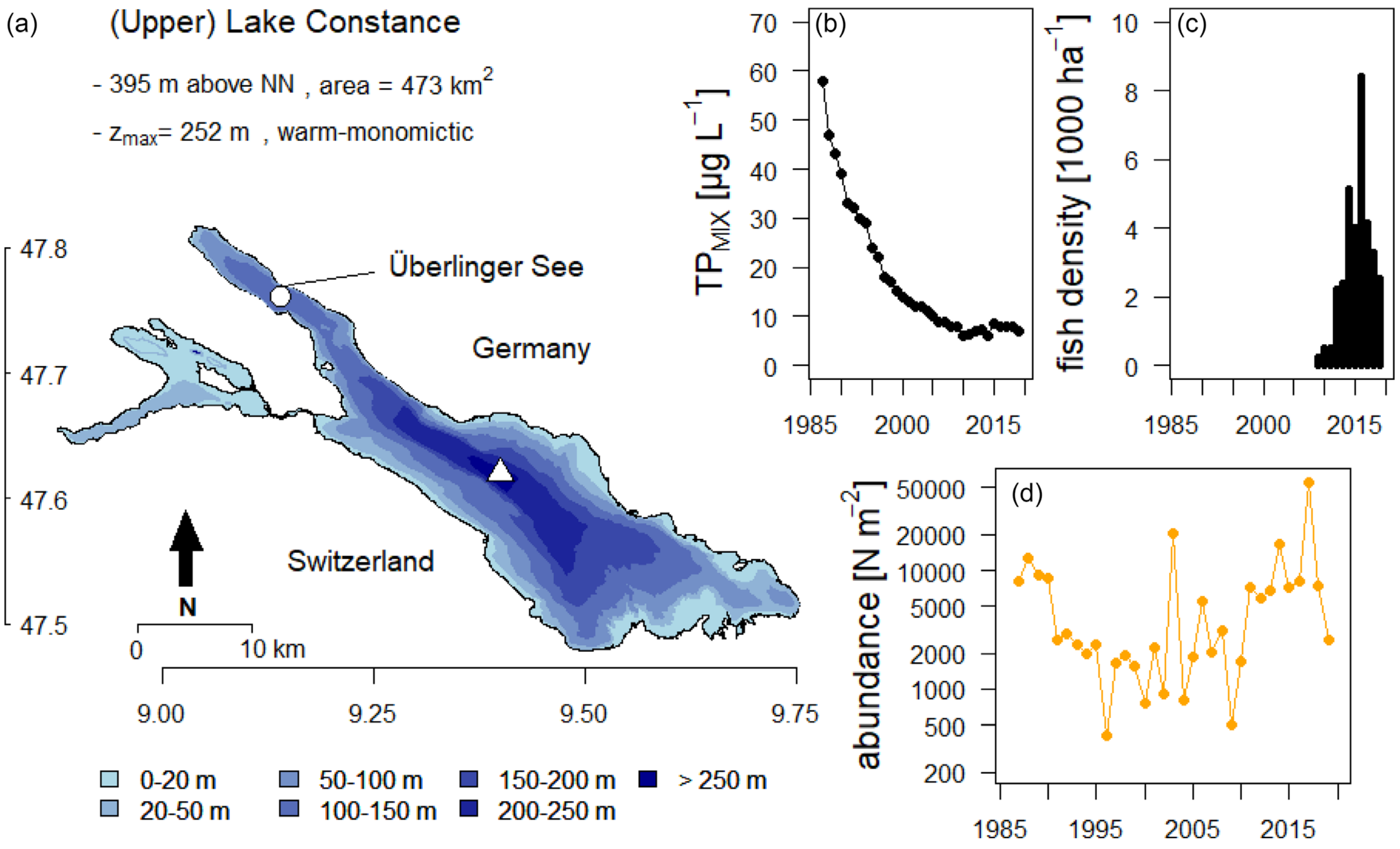

Fig. 1. (**a**) Map of Lake Constance showing the site of *Bosmina* samples within the Überlinger See (white circle), and the sampling site of measurements of total phosphorus during winter mixis (TP$_{MIX}$) (IGKB 2020) within the central basin of Upper Lake Constance (white triangle), (**b**) development of TP$_{MIX}$, (**c**) densities of small fish (Eckmann and Engesser 2019; LUBW 2021), and (**d**) geometric mean (April–August) abundances of *Bosmina* spp. during the study period. No data for fish densities are available prior to 2009.

Roughly 30 (range: 2–75) randomly selected bosminids for each month were photographed using a camera mounted to a Stemi 2000-C stereomicroscope (Carl Zeiss Werk, Göttingen, Germany), resulting in a total of 1636 pictures during the period 1987–2019. These 1636 *Bosmina* were distinguished into three species, *Bosmina coregoni*, *Bosmina longispina*, and *Bosmina longirostris*, according to the presence, length, and shape of their mucro and antennule: *B. coregoni* either lacks a clear mucro or has a very short one, accompanied by a notably elongated antennule; *B. longispina* is distinguished by its relatively long mucro and antennule, while *B. longirostris* exhibits a narrow, curved mucro and an antennule that is slightly curved toward the ventral margin (Szeroczyńska and Sarmaja-Korjonen 2007; Sakamoto and Hanazato 2008; Korosi et al. 2013). Species delineations were verified for five bosminid individuals per sample by examining the postabdominal claw using an Axiovert 40 microscope (Carl Zeiss Werk, Göttingen, Germany). The postabdominal claw morphology varies among different *Bosmina* species: *B. longirostris* exhibits a distal pecten starting at approximately one-third of the claw length with fine setules, while the basal pecten consists of 6–8 setules decreasing in size basally; *B. coregoni* features a row of robust inclined denticles in its basal part followed by a row of hair-like spines; and *B. longispina* displays a postabdominal claw with a row of rather large denticles at the basal part, continued in a group of 3–5 small-sized denticles at the base of the claws (Kotov 1996; Taylor et al. 2002; Geraldes and Alonso 2014). Body size, antennule size (anterior protuberance), mucro size (posterior protuberance), and eye diameter (Fig. 2) were measured using a self-written script in R version 4.2.2 (R Core Team 2021), and the clutch size of each *Bosmina* was recorded. Body size was measured from the posterior or end of the body, excluding the apical spine or mucro (in *B. longirostris* and *B. longispina*), to the anterior side of the *Bosmina* head. Antennule size was measured from the proximal side of the antennules fused with the rostrum to the distal sides of the antennule. Eye diameter was measured at its widest diameter. Mucro size was measured from the distal tip of the mucro to the base of the carapace along a straight line and thus includes also a part of the carapace. Thereby, mucro size is defined for all three species. Measurement of these morphological traits followed the measurement protocols of Johnsen and Raddum (1987), Kerfoot (1988), Hellsten and Stenson (1995), Kappes and Sinsch (2002).

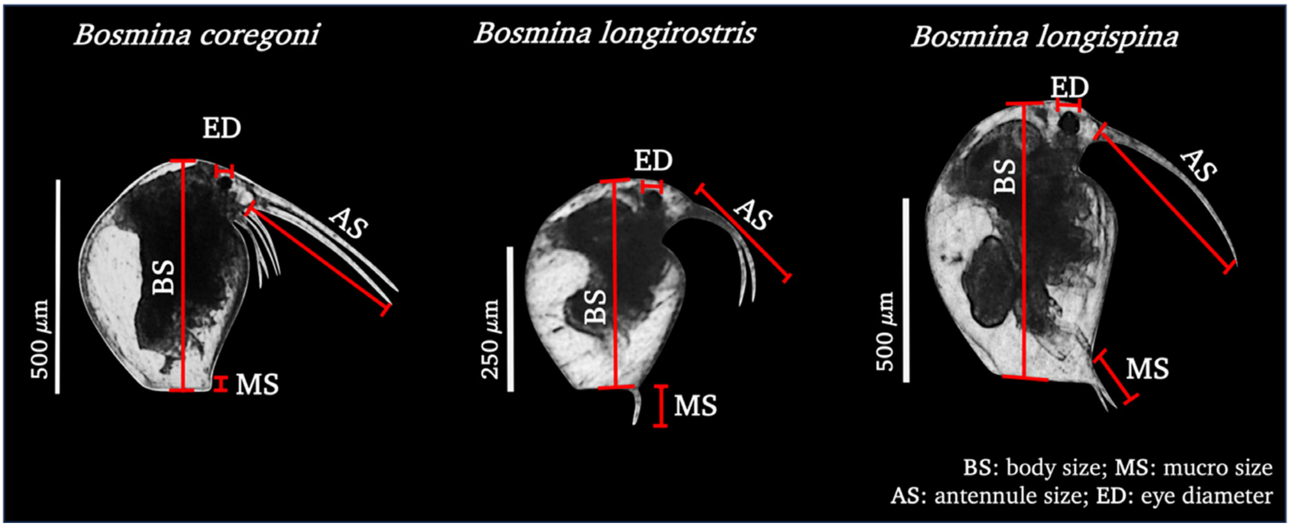

Fig. 2. Pictures of *Bosmina* spp. in Lake Constance showing the traits measured in this study: body size (BS), antennule size (AS), mucro size (MS), and eye diameter (ED).

Statistical analyses

We examined the long-term dynamics of six *Bosmina* traits both at the genus and at the species level: body size, body size of gravid females, mucro size, antennule size, eye diameter, and clutch size. Only eggs found in the brood pouch were considered in this study. To make the data suitable for analysis, we applied a $\log_{10}$ transformation to all traits except clutch size. We used Generalized Additive Mixed Models (GAMMs) with Gaussian error distribution—except for clutch size (Poisson error distribution), applying maximum likelihood (ML) (Wood and Augustin 2002; Pedersen et al. 2019). For models at the genus level, we used three predictor variables: body size (log-transformed) and the smooth functions of year and month (April, June, and August), the latter as a categorical variable. Additionally, sampling date was used as a random variable to account for non-independence of measurements during a specific sampling date. Body size was not included as a predictor in the models with body size as a dependent variable. For models examining trait dynamics at the species level, we included species as an additional factor in the models and modeled the long-term dynamics of each species as a smooth factor interaction. We did not assess whether incorporating month-specific long-term dynamics for species would improve model performance, as two of the species were not consistently observed across all 3 months. To avoid overfitting, we constrained the models by limiting the degrees of freedom or the number of knots to a maximum of 5 ($k = 5$) (Zuur et al. 2009). Normality and homogeneity of residuals for all models were examined using the mgcv::gam.check() function.

To analyze the trait dynamics of the *Bosmina* genus, we compared two GAMMs, referred to as G1 (Eq. 1) and G2 (Eq. 2), as shown below. The G1 model included body size, month, and the smooth effect of year as independent variables, while the G2 model incorporated body size, month, and the smooth effect of year stratified by month, that is, allowing for month-specific temporal trends.

$$\begin{aligned} \mathrm{G1} = \mathrm{gamm}(&\log \text{mucro size} \sim \log \text{body size} + \mathrm{month} + \mathrm{s(year)} \\ &+ \mathrm{s}(\mathrm{date}, \mathrm{bs} = \text{“re”})) \end{aligned} \tag{1}$$

$$\begin{aligned} \mathrm{G2} = \mathrm{gamm}(&\log \text{mucro size} \sim \log \text{body size} + \mathrm{month} \\ &+ \mathrm{s}(\mathrm{year}, \mathrm{by} = \mathrm{month}) + \mathrm{s}(\mathrm{date}, \mathrm{bs} = \text{“re”})) \end{aligned} \tag{2}$$

For species-level trait dynamics, we evaluated three GAMMs (S1 (Eq. 3), S2 (Eq. 4), S3 (Eq. 5)), as shown below, that accounted for the effect of species identity. S1 included species, month, and the smooth effect of year modeled separately for each species. S2 extended this by including the smooth effects of year stratified both by month and by species, while S3 included species, month, and the smooth effect of year stratified by month. All models incorporated study date as a random effect using the term s(date, bs = “re”). Models at genus vs. species levels were compared using the Akaike Information Criterion (AIC).

$$\begin{aligned} \mathrm{S1} = \mathrm{gamm}(&\log \text{mucro size} \sim \log \text{body size} + \mathrm{species} + \mathrm{month} \\ &+ \mathrm{s}(\mathrm{year}, \mathrm{by} = \mathrm{species}) + \mathrm{s}(\mathrm{date}, \mathrm{bs} = \text{‘re’})) \end{aligned} \tag{3}$$

$$\begin{aligned} \mathrm{S2} = \mathrm{gamm}(&\log \text{mucro size} \sim \log \text{body size} + \mathrm{species} + \mathrm{month} \\ &+ \mathrm{s}(\mathrm{year}, \mathrm{by} = \mathrm{month}) + \mathrm{s}(\mathrm{year}, \mathrm{by} = \mathrm{species}) \\ &+ \mathrm{s}(\mathrm{date}, \mathrm{bs} = \text{‘re’})) \end{aligned} \tag{4}$$

$$\begin{aligned} \mathrm{S3} = \mathrm{gamm}(&\log \text{mucro size} \sim \log \text{body size} + \mathrm{species} + \mathrm{month} \\ &+ \mathrm{s}(\mathrm{year}, \mathrm{by} = \mathrm{month}) + \mathrm{s}(\mathrm{date}, \mathrm{bs} = \text{‘re’})) \end{aligned} \tag{5}$$

To assess the relative contribution of species turnover and within-species trait changes to genus-level trait dynamics, we used a Venn diagram approach to partition variance. Predicted mean genus traits were calculated as the weighted average of species-specific trait means, using the relative abundance of each *Bosmina* species at each sampling date. We then compared these predicted genus means with the observed mean genus traits using regression models and variance partitioning, incorporating study month and year as categorical variables. The Venn diagram was created using the draw.circle() function from the *plotrix package* (Lemon et al. 2023) in R to illustrate how total variation in genus-level traits can be partitioned into components attributed to species turnover, within-species variation, and their interaction. All analyses were conducted using R version 4.2.2, utilizing the gamm() function from the mgcv package (Wood 2023) and the varpart() function of the vegan package (Oksanen et al. 2001).

Results

Species composition was rather stable during most of the study period, with *B. longispina* dominating, *B. longirostris* being of secondary importance, and *B. coregoni* was absent until 2008 (Fig. 3). However, in most recent years, species dominance shifted rapidly, with *B. longirostris* dominating in 2013, 2015, and 2019, *B. coregoni* in 2016 and 2017, and *B. longispina* in 2018. Long-term dynamics were rather similar in all 3 months.

Body size was smallest for *B. longirostris* (geometric mean = 330 ± 4.0 μm [SE], range = 156–595 μm), whereas the body size distributions of the *B. longispina* (508 ± 3.9 μm [SE], range = 243–923 μm) and *B. coregoni* (464 ± 7.1 μm [SE], range = 244–799 μm) strongly overlapped (Fig. 4). Mucro size *of B. coregoni* (29 ± 0.8 μm) was smallest compared to *B. longirostris* (40 ± 1.4 μm) and *B. longispina* (83 ± 0.9 μm), however, some *B. longirostris* individuals with relatively small mucro, corresponding to the *curvirostris* morphotype, were also found. Antennule size was smallest for *B. longirostris* (158 ± 2.8 μm) and strongly overlapped between *B. longispina* and *B. coregoni* (348 ± 4.1 μm). The eye size distribution of all three species showed strong overlaps (27 ± 0.5 μm) (Fig. 4c). Residuals of mucro size–body size relationships were smaller for *B. coregoni* compared to the other two species (Fig. 4d); residuals of the antennule size–body size relationship were smallest for *B. longirostris* and largest for *B. coregoni* (Fig. 4e), whereas there was large overlap between species in respect to the residuals of the eye diameter–body size relationship (Fig. 4f).

With the exception of residual antennule size, all traits showed significant long-term patterns when analyzed at the genus level (Fig. 5; Table 1b). According to the AIC, including month-specific long-term trends did not improve models for the respective traits (Table 1a). Mean body size, and especially residual mucro size, declined strongly at the end of the study period (Fig. 5a,b). Likewise, mean body size of gravid females declined during the study period (Fig. 5f). Accordingly, only 11% of gravid females were smaller than 500 μm before 2012; the percentage rose to 43% after 2011. In contrast, residuals of eye size and clutch size increased during the study period (Fig. 5d,e). Body size and residual clutch size were largest in April samples, whereas residual mucro size was smallest in April samples. For other traits, no significant differences between months were detected when not distinguishing between individual *Bosmina* species.

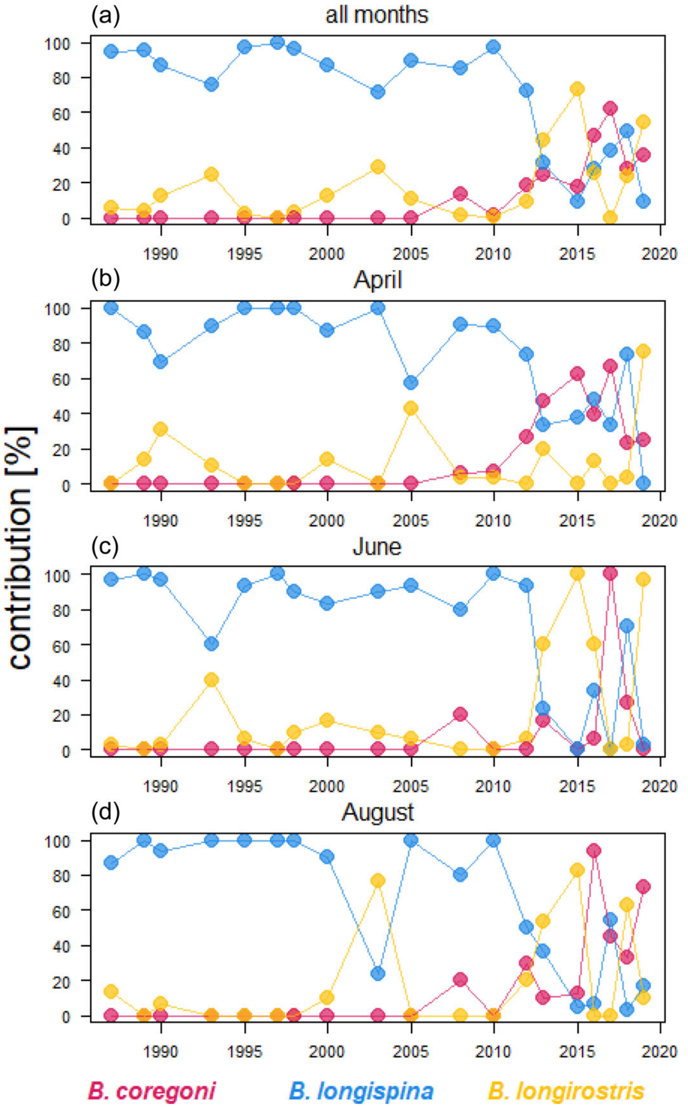

Fig. 3. Percent taxa contributions of the three *Bosmina* spp. in Lake Constance from 1987 to 2019. Taxa contributions are shown (**a**) combined across April, June and August samples in a specific year, and separately for (**b**) April, (**c**) June, and (**d**) August.

For all traits, GAMMs accounting for species differences (Table 2a) were generally superior to models not accounting for species differences (Table 1a) based on AIC (differences in

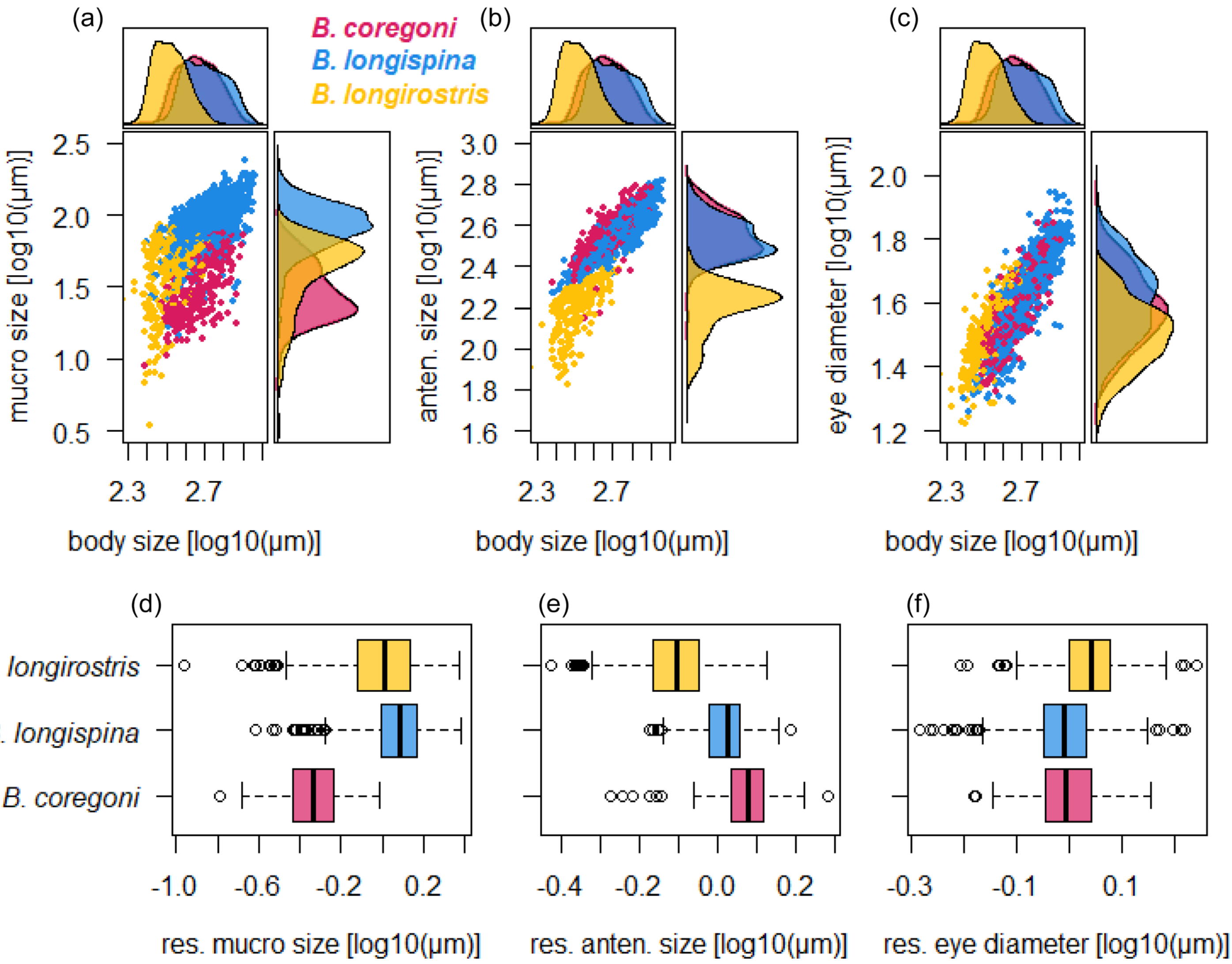

Fig. 4. Relationship of (**a**) mucro, (**b**) antennule size, and (**c**) eye diameter against body size in three species of *Bosmina* shown together with the density distributions of body sizes and traits, (**d**)–(**f**) boxplots of the residuals of the three trait—body size relationships for the three species. Body sizes and traits were $\log_{10}$ transformed.

all cases > 2). For all traits—except clutch size and body size of gravid females—at least one species showed significant long-term patterns regarding a specific trait (Table 2b). The mean body size and residual mucro size of *B. coregoni* declined, whereas the residual antennule size of this species increased (Table 2b; Fig. 6a–c). Antennule size of *B. longispina* steadily increased throughout the study period (Fig. 6b,c). Finally, *B. longirostris* showed significant temporal dynamics in residual mucro and antennule sizes, showing the smallest residual mucro and antennule during the middle of the study period (Fig. 6b,c). In addition, residual eye diameter of *B. longirostris* steadily increased (Fig. 6d).

Changes in species relative abundance had a strong effect on genus level trait variability for body size, residual mucro, and antennule sizes and the body size of gravid females (Fig. 7a–c,f), whereas residual eye diameter and clutch size could not be well predicted by relative species frequencies and mean species traits (Fig. 7d,e). Consequently, relative species frequencies had a strong effect on genus trait dynamics during the most recent study years when strong changes in relative frequencies were observed (Fig. 3). Variance partitioning of the traits, as shown by the percentage contributions in the Venn diagrams, revealed that for body size, residual mucro, and antennule sizes, as well as for the body size of gravid females, predicted trait values contributed most strongly to the observed genus traits (Fig. 7a–c,f). For residual mucro and antennule sizes, study month contributed more than 10% to the observed trait variability, highlighting the role of within-species seasonal trait variability. In contrast, for residual eye diameter, there was a large contribution of study year (23%)

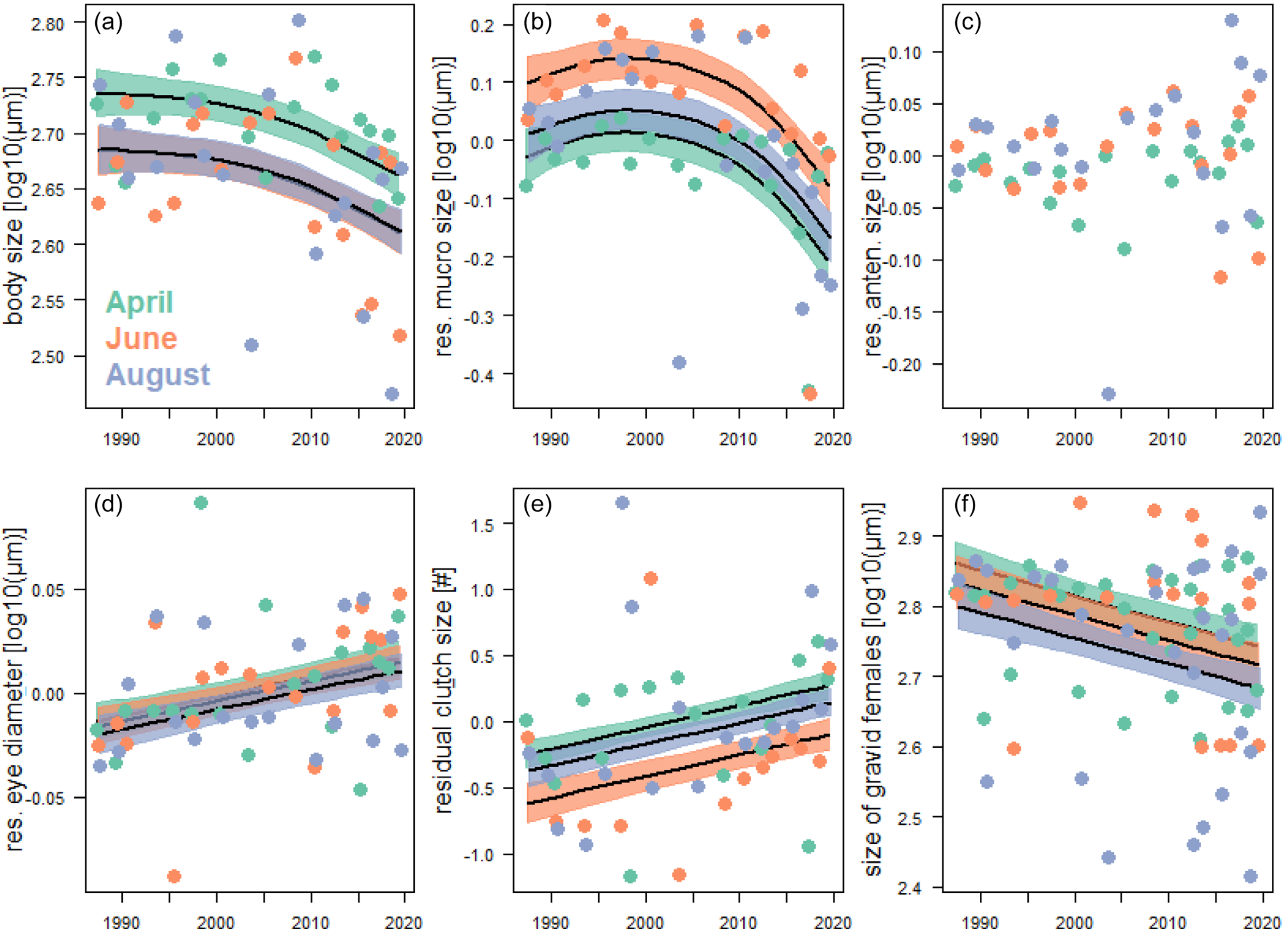

Fig. 5. *Bosmina* genus mean trait dynamics in April, June, and August (represented by the filled circles) during 1987–2019. Significant long-term patterns were found and shown (fitted values ± SE) for all traits except residual antennule size. Differences between months were observed for mean body size, mucro size, and clutch size (Table 1b). GAMM fits do show the mean long-term genus responses excluding the effects of the random factor sampling date.

suggesting consistent yearly variability of this trait. As indicated by the large residual variance, no variable could explain a substantial part of the clutch size variability.

Discussion

In this study, we explored the turnover of three *Bosmina* species, intra-specific trait variability of these species, as well as the relative importance of species turnover vs. intra-specific trait variability for genus-level trait variability during three decades of environmental changes in Lake Constance. Our results indicate that the relative influence of interspecific vs. intraspecific contributions to genus-level trait variation differed among traits. Both components increased strongly after 2012, that is, after the increase of stickleback abundances. The latter suggests that a presumed increase in top-down control more strongly affected *Bosmina* trait variability compared to two decades of oligotrophication.

Our study analyzes temporal changes in trait dynamics, but we did not link trait dynamics directly to environmental pressures such as phosphorus concentrations and fish densities. The latter was not possible because, for example, fish densities were only measured from 2009 onwards (Eckmann and Engesser 2019), that is, data did cover less than one-third of our study period. Hence, we can neither provide statistical evidence that phosphorus reduction or increased fish densities are the main drivers of *Bosmina* trait dynamics, nor can we exclude that additional drivers such as climate warming might be responsible or might have contributed to the observed patterns. However, we were able to clearly demonstrate temporal

Table 1. (**a**) The relationships between *Bosmina* traits and body size, study month, the smooth effect of study year, and the random effect of study date (s(date, bs = "re")) were evaluated using GAMMs. The tested models, G1 and G2, are ranked based on their fit to the data, as determined by the Akaike Information Criterion (AIC). The difference in AIC (dAIC) reflects the relative performance of each model compared to the best-fitting model. (**b**) Results from ANOVA are presented only for the top-performing model (G1), with significant predictors of traits indicated in bold. Significance levels are denoted as follows: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ns—not significant.

	Body size		**Mucro size**		**Antennule size**		**Eye diameter**		**Clutch size**		**Gravid female size**	
(a) Models	**dAIC**	**df**	**dAIC**	**df**	**dAIC**	**df**	**dAIC**	**df**	**dAIC**	**df**	**dAIC**	**df**
G1	0	52.1	0	55.5	0	55.6	0	49.5	0	5	0	44.1
G2	0	51.6	0.7	56.2	0.5	55.8	0.5	49.6	3.2	7	0.5	44.2

(b) ANOVA (G1)	**Body size**	**Mucro size**	**Antennule size**	**Eye diameter**	**Clutch size**	**Gravid female size**
Body size		**$F_1 = 811\ ***$**	**$F_1 = 3902\ ***$**	**$F_1 = 4398\ ***$**	**$Chi^2{}_1 = 60\ ***$**	
Month	**$F_2 = 4.6\ *$**	**$F_2 = 5.1\ **$**	$F_2 = 0.6$ ns	$F_2 = 0.12$ ns	**$Chi^2{}_2 = 6.3\ *$**	$F_2 = 1.9$ ns
s(year)	**$F_{1.5,1.6} = 4.9\ **$**	**$F_{2.4,2.5} = 11\ ***$**	$F_{1,1} = 0.08$ ns	**$F_{1,1} = 8.3\ **$**	**$Chi^2{}_{1,1} = 6.7\ **$**	**$F_{1,1} = 7.8\ **$**
s(date, bs = "re")	**$F_{45,53} = 8.0\ ***$**	**$F_{48,53} = 16\ ***$**	**$F_{49,53} = 19\ ***$**	**$F_{43,53} = 5.5\ ***$**	$Chi^2{}_{0,47} = 0$ ns	**$F_{39,47} = 11\ ***$**

Table 2. (**a**) The relationships between *Bosmina* traits and body size, study month, species identity, the smooth effect of study year for each species, and the random effect of study date (s(date, bs = "re")) were evaluated using GAMMs: S1, S2, and S3. The models (S1, S2, and S3) were ranked based on their fit to the data, as determined by the Akaike Information Criterion (AIC). The dAIC value represents the difference in AIC between each model and the best-performing model. (**b**) ANOVA results are presented only for the top-performing model (S1). Significant predictors are in bold; significance levels: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ns—not significant.

	Body size		**Mucro size**		**Antennule size**		**Eye diameter**		**Clutch size**		**Gravid female size**	
(a) Models	**dAIC**	**df**	**dAIC**	**df**	**dAIC**	**df**	**dAIC**	**df**	**dAIC**	**df**	**dAIC**	**df**
S1	0	49.7	0	68.3	0	61.6	0	50.5	0	9	0	42.6
S2	0.5	49.6	0.4	69.3	0.9	61.8	0.9	50.9	3.7	11	3.2	43.2
S3	6.1	48.1	169.7	57.1	148.8	56.2	3.1	49.3	1.5	9	4.5	40

(b) ANOVA (S1)	**Body size**	**Mucro size**	**Antennule size**	**Eye diameter**	**Clutch size**	**Gravid female size**
Body size		**$F_1 = 945***$**	**$F_1 = 4172***$**	**$F_1 = 4351***$**	**$Chi^2{}_1 = 58***$**	
Month	**$F_2 = 4.5*$**	**$F_2 = 7.8***$**	**$F_2 = 5.4**$**	$F_2 = 0.36$ ns	**$Chi^2{}_2 = 9**$**	**$F_2 = 6.5**$**
Species	**$F_2 = 201***$**	**$F_2 = 23***$**	**$F_2 = 476***$**	**$F_2 = 49***$**	**$Chi^2{}_2 = 18***$**	**$F_2 = 220***$**
s(year): *B. Coregoni*	**$F_{1,1} = 11**$**	**$F_{3,3} = 11***$**	**$F_{1,1} = 18***$**	$F_{1,1} = 0.08$ ns	$Chi^2{}_{1,1} = 2.7$ ns	$F_{1,1} = 0.09$ ns
s(year): *B. Longispina*	$F_{1,1} = 0.04$ ns	$F_{2,2} = 1.7$ ns	**$F_{1,1} = 15***$**	$F_{1,1} = 1.8$ ns	$Chi^2{}_{1,1} = 0.9$ ns	$F_{1,1} = 2.1$ ns
s(year): *B. Longirostris*	$F_{1,1} = 0.8$ ns	**$F_{7,8} = 14***$**	**$F_{7,8} = 16***$**	**$F_{1,1} = 12***$**	$Chi^2{}_{1,1} = 0.2$ ns	$F_{1,1} = 2.7$ ns
s(date, bs = "re")	**$F_{40,53} = 4.1***$**	**$F_{46,53} = 7.9***$**	**$F_{44,53} = 6***$**	**$F_{40,53} = 4.0***$**	$Chi^2{}_{0,47} = 0.001$ ns	**$F_{33,47} = 3.6***$**

changes of *Bosmina* traits at genus and species levels and relate these patterns to the dominant drivers of food web changes in Lake Constance during the last decades.

Phosphorus levels in Lake Constance started to decline in the early 1980s and had striking effects on phytoplankton (Jochimsen et al. 2013; Pranger et al. 2025), zooplankton (Straile 2015), and pelagic fish (DeWeber et al. 2022). However, despite a strong decline in phosphorus concentrations during 1987–2006, the relative species composition of *Bosmina* remained largely unchanged, even though densities declined until the mid-1990s. This is contrary to common patterns observed during periods of nutrient changes in various lakes (Løvik and Kjellberg 2003), and also during eutrophication in Lake Constance (Hofmann 1998). Our findings suggest that oligotrophication did not lead to increased food limitation for bosminids during the study period based on the absence of a long-term decrease in clutch sizes and the increase of eye sizes of *Bosmina*. Decreases in both clutch size (Lynch 1977; Sodré and Bozelli 2019) and eye size (Brandon and Dudycha 2014) have been shown to be related to food limitation in cladocerans. The increase of eye size might thus even point to an increasing amount of resources

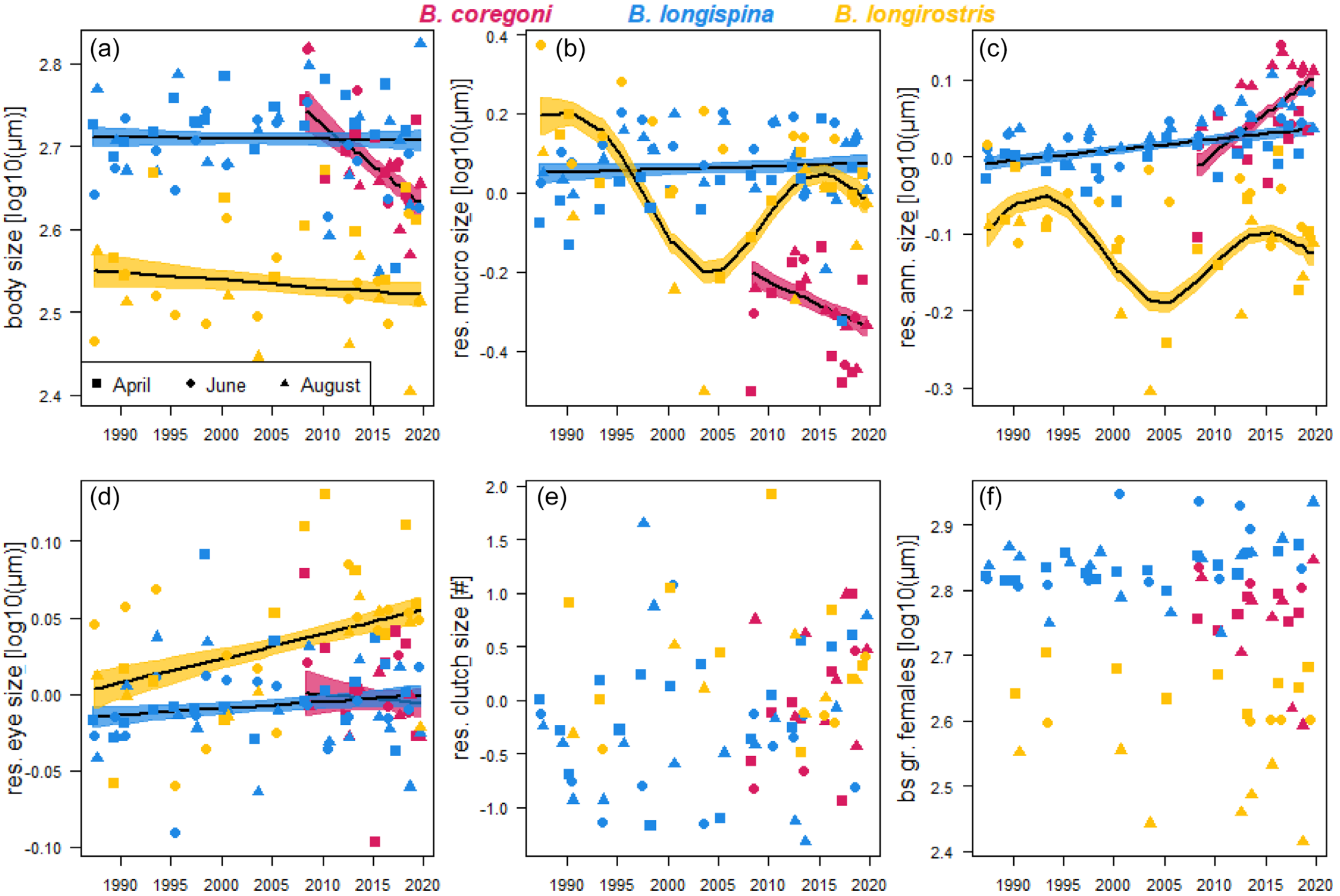

Fig. 6. *Bosmina* species trait dynamics during 1987–2019. Significant long-term patterns for at least one species were found for all traits except clutch size and body size of gravid females (Table 2b). GAMM fits (± SE) (curves) do show the mean long-term responses for each species excluding the effects of the random factor sampling date and differences between months. The filled shapes represent average data points corresponding to the three study months, with squares indicating April, circles representing June, and triangles denoting August.

during the study period potentially caused by reduced competition due to declining *Daphnia* abundances (Straile 2015).

The increase of small fish in 2012 was largely due to a documented increase of sticklebacks, as supported by both hydroacoustic surveys and fish catches (Alexander et al. 2016; Gugele et al. 2020) and data on stickleback bycatch in whitefish netting (Rösch et al. 2018). Furthermore, after 2012, large changes in the zooplankton community occurred, such as increases of small zooplankton, including *Bosmina* and *Daphnia cucullata* (Maier et al. 2023). Likewise, growth of pelagic whitefish strongly decreased after 2012, presumably due to increased competition with sticklebacks (Rösch et al. 2018). The increase of small zooplankton species, a typical result of increased predation (e.g., Brooks and Dodson 1965), suggests that the combined predation pressure by whitefish and sticklebacks increased due to the disproportionate rise of sticklebacks. Our study shows that simultaneously with the increase of sticklebacks in 2012, rapid species turnover within *Bosmina*, linked to a decrease in overall *Bosmina* body size and among gravid females, occurred. The observed reductions align with expectations under increased fish predation (Brooks and Dodson 1965; Dodson 1974; Korosi et al. 2013). After 2012, the largest species, *B. longispina*, saw a decline in relative frequency, while the smaller *B. longirostris* began to rise. Similar shifts in *Bosmina* size structure have been observed in Norwegian lakes experiencing increased planktivory (Amundsen et al. 2009). However, in the Norwegian lakes, the increase in planktivory was due to the introduction of vendace, whereas in Lake Constance the presumed rise in planktivory was due to the increasing number of sticklebacks. The subsequent rise of *B. coregoni*—larger than *B. longirostris*—suggests that factors beyond selection for smallest body size, such as alterations in the food web induced by fish, also played crucial roles. A variety of experiments demonstrated that predators present in Lake Constance, such as copepods (Kerfoot 2006; McNaught and Weber 2009), *Leptodora* (Hellsten et al. 1999; Lagergren

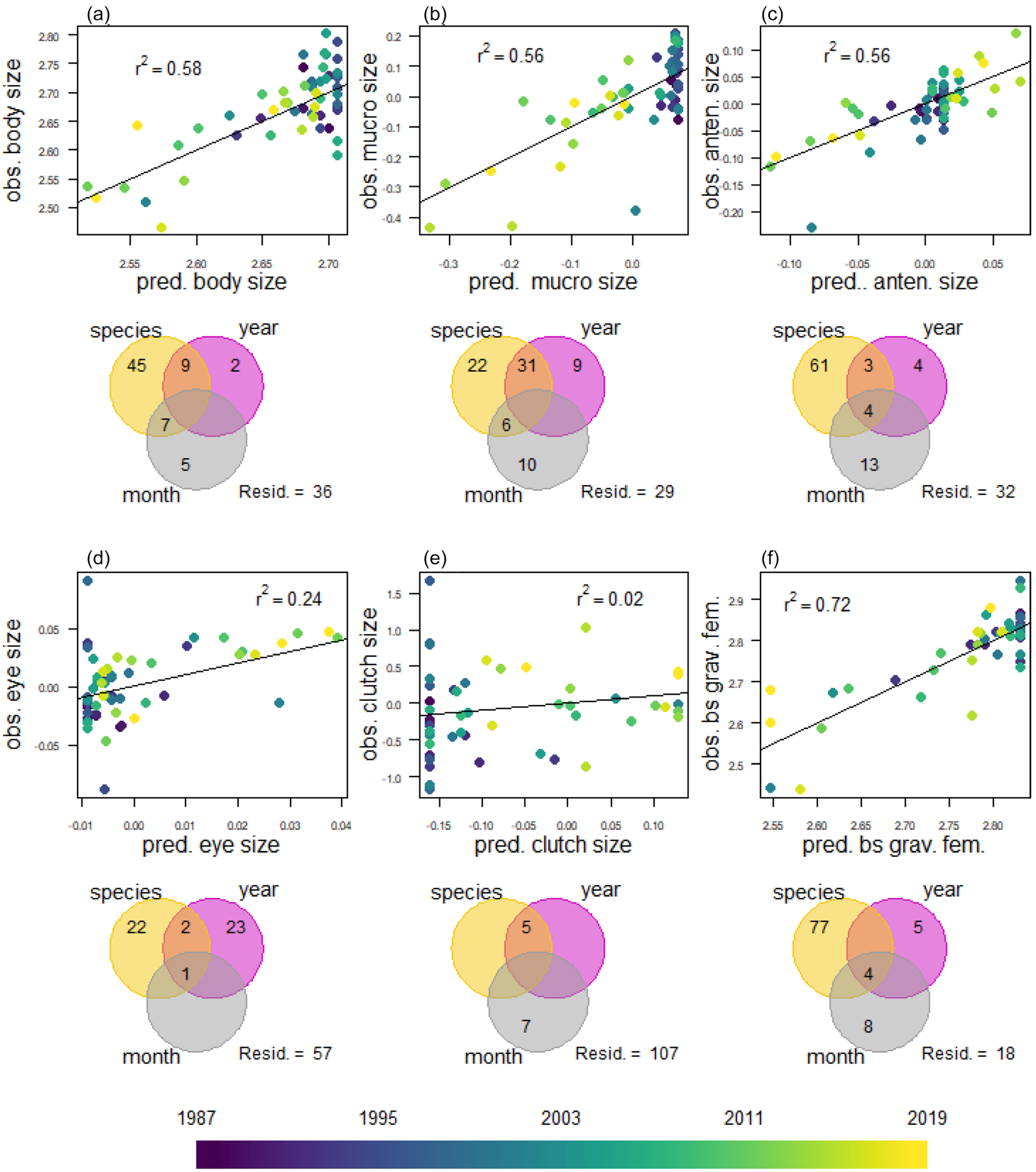

Fig. 7. Legend on next page.

and Stenson 2000; McNaught and Weber 2009), and *Bythotrephes* (Pangle et al. 2007; Baludo 2024), can influence mucro and antennule sizes of various *Bosmina* species. Based on our data, it is not possible to examine the role of invertebrate predators for the observed intra-specific trait changes. In contrast, we did not find any studies providing experimental evidence of fish influencing *Bosmina* morphology; however, intraspecific declines in antennule size have been suggested to be due to fish predation (Black and Hairston 1983). This suggests that a food-web approach would be needed to disentangle the causes behind the complexity of trait dynamics of *Bosmina*.

Species fluctuations strongly influenced most traits, especially those that showed large interspecific differences such as antennule size and mucro size. For example, with the increase of *B. coregoni*, which has the smallest mucro size, the overall mucro size at the genus level declined. Likewise, species turnover from *B. longispina* (medium-sized residual antennule) to *B. longirostris* (small residual antennule) and eventually *B. coregoni* (large residual antennule) after 2012 resulted in rapid interannual shifts in genus mean antennule size. In contrast, traits with minor interspecific differences such as eye sizes were less influenced by species turnover and more so due to long-term intraspecific trait changes. Intraspecific variability also contributed strongly to monthly changes in mucro and antennule sizes at the genus level, reflecting often the documented cyclomorphological seasonal change of these traits (Black and Hairston 1983; Hellsten and Stenson 1995) and rather small differences in species composition between months. These examples show that genus-level traits calculated without considering within-species trait variability will provide reliable information in cases of strong species fluctuations and large intraspecific trait variability, but less so when species fluctuate less and show small trait differences.

Our study shows that the relationship between species level and higher level trait variability is complex and trait-dependent—even at low aggregation such as at genus level. In the case of eye size, the long-term increase of residual eye size of *B. longirostris* strengthened the weak effect of species fluctuations on genus level eye size dynamics. In contrast, trends in residual clutch size and body size of gravid females were largely driven by species fluctuations, while for these traits no within-species trends in size variability were observed. Finally, antennule size dynamics were characterized by rapid dynamics during the years since 2012, with species trait dynamics enlarging genus level trait variability, that is, antennule of the species with large antennule (*B. coregoni*) increased, whereas antennule of the species with small antennule (*B. longirostris*) tended to decrease. These diverging intraspecific trends contributed to increased variability at the genus level and obscured a clear temporal pattern, even though significant temporal trends were observed at the species level.

To conclude, this is the first study examining the role of species vs. genus level trait dynamics for an important zooplankton herbivore genus, *Bosmina*, during three decades of environmental change. We show that during two decades of oligotrophication no large changes were observed, whereas presumably, direct and indirect effects of fish predation resulted in rapid species replacements in *Bosmina* spp. and trait changes at both the species and genus levels. For most traits, species turnover was the most important factor determining genus level long-term trait dynamics; however, within-species trait variability played a larger role for seasonal genus-level variability. Furthermore, whether within-species trait variability enhanced or weakened genus level variability due to species fluctuations depended on the trait under consideration. Further research is needed to unravel the complex interplay of the various environmental pressures driving these intriguing dynamics within *Bosmina* populations.

Author Contributions

Marjohn Yucada Baludo: Conceptualization (equal); data curation (lead); formal analysis (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Dietmar Straile:** Conceptualization (equal); formal analysis (equal); funding acquisition (lead); methodology (equal); project administration (lead); supervision (lead); writing – review and editing (equal).

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Fig. 7. Genus-level trait dynamics and their drivers. Panels **a**–**f** show scatter plots of predicted vs. observed genus trait values. The R^2 value indicates the proportion of variance explained by the model. The Venn diagrams below each plot show the percentage contribution of three factors (species, year, and month) to the observed trait variability. "Resid" indicates the percentage of unexplained residual variance. Note the strong predictive power of the models for traits like body size (a, $R^2 = 0.58$) and body size of gravid females (f, $R^2 = 0.72$), where species composition is a primary driver. In contrast, traits like eye diameter (d, $R^2 = 0.24$) and clutch size (e, $R^2 = 0.02$) are poorly predicted by these factors, with a large contribution of unexplained variance (57% and 107%, respectively). Predicted mean genus traits are based on relative frequencies of species and mean trait values for each species. Except for clutch size, all traits and residuals were calculated from $\log_{10}$-transformed trait values. Negative values and residual variability exceeding 100% due to covariation between predictor variables are not shown.

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Data Availability Statement

Data in this study are accessible through the research data repository of the University of Konstanz, KonDATA: https://kondata.uni-konstanz.de/radar/en/dataset/csdqtzddt6a6fnq7.

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