Coupled changes in traits and biomasses cascading through a tritrophic plankton food web

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Abstract

Trait-based approaches have broadened our understanding of how the composition of ecological communities responds to environmental drivers. This research has mainly focussed on abiotic factors and competition determining the community trait distribution, while effects of trophic interactions on trait dynamics, if considered at all, have been studied for two trophic levels at maximum. However, natural food webs are typically at least tritrophic. This enables indirect interactions of traits and biomasses among multiple trophic levels leading to underexplored effects on food web dynamics. Here, we demonstrate the occurrence of mutual trait adjustment among three trophic levels in a natural plankton food web (Lake Constance) and in a corresponding mathematical model. We found highly recurrent seasonal biomass and trait dynamics, where herbivorous zooplankton increased its size, and thus its ability to counter phytoplankton defense, before phytoplankton defense actually increased. This is contrary to predictions from bitrophic systems where counter-defense of the consumer is a reaction to prey defense. In contrast, counter-defense of carnivores by size adjustment followed the defense of herbivores as expected. By combining observations and model simulations, we show how the reversed trait dynamics at the two lower trophic levels result from a "trophic biomass–trait cascade" driven by the carnivores. Trait adjustment between two trophic levels can therefore be altered by biomass or trait changes of adjacent trophic levels. Hence, analyses of only pairwise trait adjustment can be misleading in natural food webs, while multitrophic trait-based approaches capture indirect biomass–trait interactions among multiple trophic levels.

Ecological communities are commonly composed of many species, each being connected by a large number of interactions with other species and their environment. The resulting high complexity of communities makes it difficult to understand what determines their composition and to predict their reorganization under environmental changes. In the last two decades, trait-based approaches have increasingly served as a productive tool to cope with these problems by grouping organisms according to their functional traits rather than their species identity, which reduces the complexity to a

manageable, mechanistic level. Functional traits are well-defined, measurable, taxa-transcending properties of organisms that strongly influence their fitness (McGill et al. 2006; Westoby and Wright 2006). Originally coming from terrestrial plant ecology, trait-based approaches have been transferred also to the aquatic realm (Weithoff 2003; Litchman et al. 2007) enhancing a mechanistic understanding of the relationship between community structure/functioning and environmental conditions (Kremer et al. 2017; Kiørboe et al. 2018).

In aquatic ecology, trait-based approaches have been applied across many taxa (Kremer et al. 2017), including bacteria (Brown et al. 2014), phytoplankton (Weithoff 2003; Litchman and Klausmeier 2008), zooplankton (Litchman et al. 2013; Hébert et al. 2016), benthic invertebrates (Bremner et al. 2003), and fish (Erös et al. 2009). Recent research in that field has analyzed seasonal trait succession of phytoplankton within one ecosystem (Edwards et al. 2013a; Terseleer et al. 2014) or has compared the trait composition of plankton communities across different environments (Barton et al. 2013; Edwards et al. 2013b; Brun et al. 2016; Klais et al. 2017). These studies typically examined how the trait composition within only one trophic level, e.g., phytoplankton, responds to abiotic (e.g., temperature, light, and nutrients) or biotic drivers

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(e.g., competition, prey availability, and grazing). However, they did not consider how different trophic levels mutually affect their trait composition and neglected feedbacks of trait changes on their drivers.

Conceptually, trait changes within a trophic level may emerge, for example, from phenotypic plasticity at the individual level, from mutation and sorting of different genotypes of the same species, or from sorting of different species. All these processes contribute to the trait changes observed within a trophic level, although the major trait shifts in plankton food webs likely result from species sorting, given the large interspecific trait variation, for example, in phytoplankton size (Finkel et al. 2010). If species are functionally very similar and share similar traits, they can be classified into functional groups (Reynolds et al. 2002). Changes in the relative contribution of such functional groups to the total trophic level biomass also reflect trait adjustment (Fig. 1).

Trophic interactions crucially affect the fitness of organisms in almost every ecosystem and thus have a high potential to drive trait changes in communities. In phytoplankton communities, for example, a high predation pressure by herbivorous zooplankton usually suppresses edible species and selects for defended species (Agrawal 1998; Tessier and Woodruff 2002; Steiner 2003). Favorable defense strategies include, for example, a larger size, a higher swimming speed, toxicity or colony formation (Pančić and Kiørboe 2018). Herbivorous

zooplankton may act as keystone predators in such systems, allowing for stable coexistence of edible species, which are often the superior resource competitors, and less competitive but less edible species (Grover 1995; Leibold 1996; Steiner 2003). However, trait variation and adjustment are not restricted to the basal trophic level. Thus, an enhanced defense level of phytoplankton may, in turn, lead to a strong selection of zooplankton strategies to overcome prey defense, i.e., promoting species with counter-defenses, like an alternative feeding mode, an increased foraging activity or size (Boukal 2014). This induces further trait changes in the prey community, which can be considered as an "arms race between communities" (Våge et al. 2018). We commonly assume that the counter-defense trait of predators follows the defense trait of their prey in such "arms races," as visualized in Fig. 1.

Trade-offs may play a central role in organizing these trait dynamics. For example, less defended prey species take over at decreasing predator biomasses, given their lower costs regarding growth (Fig. 1). The reduced defense level of the prey, in turn, promote predators with a lower counter-defense, but higher grazing rate (Fig. 1). Thus, the trait and biomass dynamics of trophic levels may interact and may produce so-called "biomass–trait feedbacks" (Fig. 1) (Klauschies et al. 2016), analogous to eco-evolutionary feedbacks in case of purely genetic, intraspecific trait changes (Fussmann et al. 2007; Post and Palkovacs 2009).
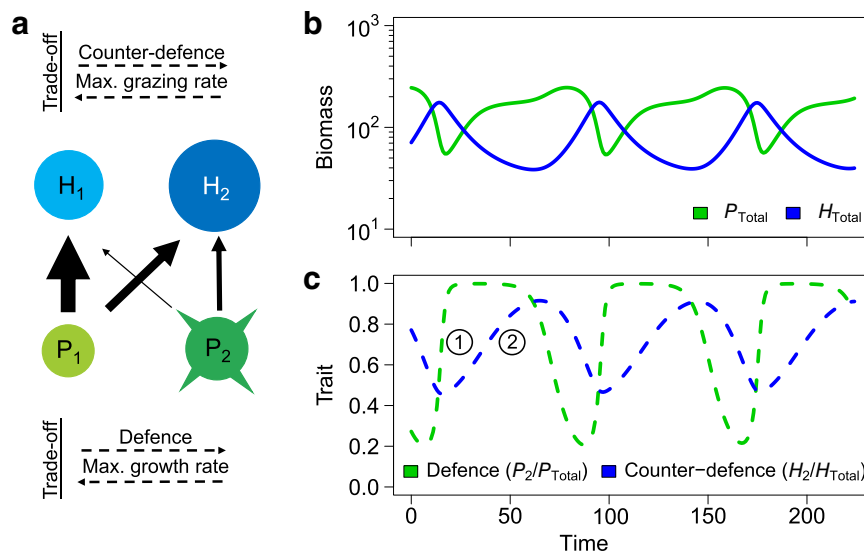

Fig 1 (**a**) Food web model of two co-adjusting trophic levels, that is, primary producers P and herbivores H, and (**b**) their predicted biomass and (**c**) trait dynamics. (**a**) Each trophic level is divided into two types (e.g., functional groups) reflecting trait differences: Undefended (P_1) and defended primary producers (P_2), and herbivores without (H_1) and with counter-defense (H_2). Defense trades off with maximum growth rate and counter-defense with maximum grazing rate (as indicated by dashed arrows). The strength of trophic interactions among the types is indicated by the thickness of the solid arrows. (**b**) The biomasses of the two trophic levels cycle, where P_{Total} denotes the total primary producer and H_{Total} the total herbivore biomass. (**c**) Cycles occur also in the traits, with defense of primary producers increasing first ① followed by the counter-defense of herbivores ②. Biomass and trait dynamics feedback on each other, for example, an increasing herbivore biomass initiates an increase of primary producer defense which, in turn, contributes to the decrease of herbivore biomass.

Only a few trait-based studies have shown empirically so far how two trophic levels mutually affected their trait composition. Kenitz et al. (2017) demonstrated how motility in protists and the foraging mode of copepods mutually affected each other and changed within a seasonal cycle. Tirok and Gaedke (2010) found similar patterns of trait adjustment between phytoplankton and ciliate communities. However, natural food webs usually comprise more than two trophic levels and each of them can interact with the others directly or indirectly (e.g., in a trophic cascade) via changes in biomasses or trait composition (Leibold et al. 1997; Schmitz et al. 2004; Vadstein et al. 2004; Zöllner et al. 2009; Ceulemans et al. 2019). In such multitrophic systems, indirect effects may emerge, for example between carnivores and primary producers, with underexplored consequences for their biomass and trait dynamics and related ecosystem functions. In this study, we analyze the biomass and trait dynamics in a natural multi-trophic food web, and then compare the observed patterns with a model concerning three trophic levels divided into different functional groups (Fig. 2).

We use long-term data from large, deep Lake Constance with high-frequency biomass measurements of three trophic levels, namely phytoplankton, herbivorous and carnivorous zooplankton. We assign the species at each trophic level to two functional groups based on species-specific trait

measurements, mainly body size, and well-known trophic relationships (Fig. 2). An altered relative contribution of a functional group to the total biomass of the respective trophic level implies changes in the mean trait value of that level. Across 10 years of measurements, we observed pronounced, highly recurrent changes in total biomasses and mean trait values at all trophic levels within the growing season, which were largely driven by biotic factors. Remarkably, the temporal order of trait changes between the two lower trophic levels was reversed compared to predictions on bitrophic systems: the herbivores increased in size, and thus in their ability to counter phytoplankton defense, before phytoplankton defense actually increased. A food web model reproduced the observed dynamics and showed that this reversed order was driven by the grazing impact of the third trophic level: initially dominant small carnivores (cyclopoid copepods), feeding on and suppressing small herbivores such as ciliates, promote larger herbivores (e.g., daphnids). The subsequently high biomasses of large herbivores only then selects for phytoplankton defense, although phytoplankton defense is less effective with increasing sizes of the herbivores. We refer to this phenomenon as a "trophic biomass–trait cascade." Our results demonstrate that the analysis of pairwise trait adjustment can be misleading in natural food webs, while multi-trophic trait-based approaches are suitable to obtain mechanistic understanding of community trait dynamics.

Methods

Study site and plankton data

Lake Constance is a temperate, large (472 km²), deep (mean depth = 101 m), warm-monomictic lake north of the European Alps, which was meso-trophic during the study period. Plankton data were collected weekly during the growing season and approximately every 2 weeks in winter from different depths. We used the data from the uppermost layer between 0 and 20 m depth, roughly corresponding to the epilimnion and euphotic zone. Plankton abundances were determined by microscopic counts and were converted to biomasses based on measurements of organism size and specific carbon to volume or length relationships. For details *see* Gaedke (1992) and literature cited therein, except for phytoplankton carbon conversion *see* Menden-Deuer and Lessard (2000).

We considered biomass data of phytoplankton, herbivorous and carnivorous zooplankton from 1987 to 1996, representing the main body of the first three trophic levels in the lake (Gaedke et al. 2002; Boit and Gaedke 2014). Weekly resolved biomass measurements on fish at the third and higher trophic levels were not available. However, it was estimated for the considered growing season that the grazing losses of even large herbivores (e.g., daphnids) resulted mainly from grazing by carnivorous cladocerans (around 80%) and not from fish (Gaedke and Straile 1994). Lake Constance has been intensively fished, which has likely reduced the grazing impact of
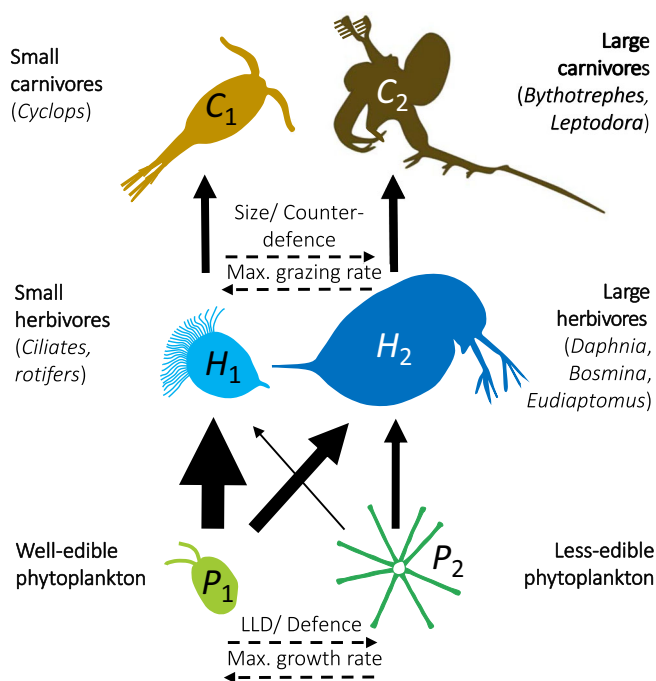

Fig. 2. Simplified plankton food web with two functional groups at each of the three trophic levels considered. Solid arrows represent trophic interactions where their thickness indicates the strength of the feeding link, given by the preference of the respective predator. Dashed arrows show the direction in which the respective trait values at the two lower trophic levels increase.

fish on plankton (Boit and Gaedke 2014). Hence, we focus here on the plankton dynamics and discuss potential effects of fish later (cf. "Discussion" section).

The plankton biomass data were averaged across years using a biweekly resolution in order to obtain general insights on recurring seasonal patterns. We standardized the time axis relative to the onset of the clear-water phase (CWP), the distinctive, grazing-induced biomass minimum of phytoplankton in early summer. This standardization accounts for differences in winter and early spring weather conditions, which represent the dominant source of interannual variability and affect the timing of the CWP in this lake (Straile 2000). We excluded the winter season where mainly physical factors like irradience, vertical mixing, and temperature determine plankton growth and focussed on the growing season with trophic interactions acting as main drivers of the plankton dynamics (Sommer et al. 2012). The growing season was defined here as the period from 12 weeks before the CWP to 20 weeks after the CWP, corresponding approximately to the period from March to early November.

Traits, trade-offs, and functional groups

We distinguished between two functional groups at each of the three trophic levels based on species-specific lab measurements of traits characterizing the trophic interactions of the organisms and their growth/grazing capability. Ensuing from this functional classification, we built a simplified food web model comprising the major feeding links among these groups (Fig. 2). This allowed us to theoretically approach grazing-driven trait changes within each trophic level, which can be tracked by shifts in the relative contribution of the functional groups. Phytoplankton was divided into well-edible P_1 and less-edible phytoplankton P_2 based on feeding experiments conducted with Lake Constance plankton (Knisely and Geller 1986). If required, non-tested algal species were categorized according to their longest linear dimension LLD (larger algae are less-edible), shape and colony formation. The phytoplankton faces an interspecific trade-off between defense and growth (Wirtz and Eckhardt 1996; Ehrlich et al. 2020). Hence, the lower edibility of P_2 for herbivores comes at the cost of a lower maximum weight-specific growth rate compared to P_1.

The herbivorous zooplankton was classified into small herbivores H_1, comprising ciliates and rotifers, and large herbivores H_2, consisting of predominantly herbivorous crustaceans (*Daphnia*, another cladoceran *Bosmina* and the calanoid copepod *Eudiaptomus*). H_1 feeds almost entirely on well-edible algae. In contrast, H_2 has a larger prey spectrum (i.e., generality) which covers also a considerable amount of the less-edible algae, implying a counter-defense (*see* Fig. 2). The counter-defense of large herbivores trades off with a lower weight-specific grazing rate compared to H_1 (de Castro and Gaedke 2008).

At the third trophic level, we distinguished between small carnivores C_1, made up of cyclopoid copepods, and large carnivores C_2, which were the cladocerans *Leptodora kindtii* and *Bythotrephes longimanus*. For simplicity, we assumed that C_1 feeds exclusively on H_1 and C_2 on H_2 (Fig. 2). In reality, C_1 is omnivorous because at least the nauplii consume phytoplankton. However, the contribution of nauplii to total copepod biomass and the contribution of C_1 to phytoplankton grazing are minor (Gaedke 1992; Tirok and Gaedke 2006). As we want to focus on the main feeding interactions driving trait changes, we disregard the link from phytoplankton to C_1.

Food web model

We set up a food web model comprising the main feeding links among the six previously described functional groups (Fig. 2). The biomass dynamics of P_1, P_2, H_1, H_2, C_1, and C_2 are given by

$$\frac{dP_i}{dt} = r_i P_i \left(1 - \frac{P_1 + P_2}{K}\right) - \sum_{j=1}^{2} \frac{G_j p_{ij} P_i H_j}{h + \sum_{i=1}^{2} p_{ij} P_i} - dP_i$$

$$\frac{dH_j}{dt} = \varepsilon \frac{G_j \sum_{i=1}^{2} p_{ij} P_i}{h + \sum_{i=1}^{2} p_{ij} P_i} H_j - a_j H_j C_j \qquad (1)$$

$$\frac{dC_j}{dt} = \varepsilon a_j H_j C_j - m_j C_j^2.$$

The definitions, (initial) values and units of the state variable and parameters are provided in Table 1. We assume logistic growth of phytoplankton, mimicking competition for nutrients and light, with all Lotka-Volterra competition coefficients equal to one. Both phytoplankton groups share the same values of the carrying capacity K and natural mortality d, but differ in their maximum weight-specific growth rate r_i (Table 1). Hence, the phytoplankton group with the highest r_i, well-edible phytoplankton P_1, would outcompete the other one in the absence of predation. Given the phytoplankton growth-defense trade-off, a higher r_i comes at the cost of higher edibility values p_{ij} (probability of being attacked) for the different herbivore groups j (Table 1). The grazing of herbivores on phytoplankton is described by a two-prey type Holling type II functional response. The herbivore groups differ in their maximum weight-specific grazing rates G_j and their preferences for the different phytoplankton groups which is reflected in the different p_{ij} values (Table 1). For simplicity, we assume equal half-saturation constants h for H_1 and H_2, and equal conversion efficiencies ϵ for H_1, H_2, C_1, and C_2.

To keep the model complexity at a minimum, we assume a linear functional response of carnivores, where the weight-specific clearance rate a_j of C_1 is higher than for C_2. The

Table 1 State variables and parameters.

Var./ Par.	Definition	Value (at T_{max} for r_i, G_j, a_j, m_j)	Unit	Source
P_i	Biomass of phytoplankton group i	Initial: $P_1 = 12$, $P_2 = 8$	mg C m^{-3}	Own data*
H_j	Biomass of herbivorous zooplankton group j	Initial: $H_1 = 4$, $H_2 = 5$	mg C m^{-3}	Own data*
C_j	Biomass of carnivorous zooplankton group j	Initial: $C_1 = 10$, $C_2 = 0.1$	mg C m^{-3}	Own data*
r_i	Max. weight-specific growth rate of P_i	$r_1 = 1.4$, $r_2 = 0.9$	d^{-1}	Bruggeman (2011)
K	Carrying capacity of P_i	400	mg C m^{-3}	Estimated from own data*
d	Natural mortality of P_i	0.1	d^{-1}	Sommer (1984)
p_{ij}	Edibility of P_i for H_j	$p_{11} = 1.0$, $p_{21} = 0.1$, $p_{12} = 1.0$, $p_{22} = 0.4$		Knisely and Geller (1986)
G_j	Max. weight-specific grazing rate of H_j	$G_1 = 1.2$, $G_2 = 0.6$	d^{-1}	Production to biomass ratios[†]
h	Half-saturation constant	120	mg C m^{-3}	Estimated from own data*
ϵ	Conversion efficiency	0.3		Straile (1997)
a_j	Weight-specific clearance rate of C_j for H_j	$a_1 = 0.016$ (≈ 0.001–0.04), $a_2 = 0.003$	d^{-1}(mg C m^{-3})$^{-1}$	Santer (1993) Plaβmann et al. (1997) Hansen (2000)[‡]; Havel (1985)[§]
m_j	Weight-specific mortality rate of C_j	$m_1 = 0.001$, $m_2 = 0.007$	d^{-1}(mg C m^{-3})$^{-1}$	Manually fitted
T_{max}	Max. temperature of growing season	16	°C	Measured (around early August)
Q_{10}	Temperature coefficient	For r_i, G_1 : 1.5 For G_2, a_j, m_j : 2.5		Sherman et al. (2016); Burns (1969)
t_{end}	Period of growing season	225	d	Own data*

*Measured biomasses (Fig. 3a,b), for details *see* Boit and Gaedke (2014) and literature cited therein.
[†]Obtained from direct measurements and a mass-balanced flow model developed for Lake Constance (Gaedke et al. 2002). The maximum *P/B* ratios, representing maximum weight-specific growth rates, were divided by ϵ to estimate G_j values.
[‡]For a_1, clearance rates measured for *C. vicinus*, the dominant cyclopoid copepod during spring, were divided by its body carbon weight. The a_1-range given in brackets was used for the model sensitivity analysis and reflects the range found in the literature, when assuming different body weights (≈ 2–10 μg C) based on George (1976) and own measurements.
[§]Clearance rate measured for *L. kindtii* divided by its body weight taken from Branstrator (2005).

carnivores are exposed to a density-dependent mortality which mimics, among others, grazing losses by fish predation. The ambient mortality rate is the product of the weight-specific mortality rate m_j and the ambient biomass of the respective carnivore group. That is, the mortality rate increases linearly with increasing biomass. We assume that m_j is higher for large carnivores, as they are preferred by dominant fish species (Straile and Hälbich 2000).

The model was run within one growing season. Mean temperatures in the uppermost 20 m varied from ca. 4–16°C within the growing season which is described by

$$T = 6\sin\left(1.4\pi\frac{t}{t_{end}} - 1.5\right) + 10 \tag{2}$$

in the model, fitting the measured temperature dynamics (Fig. S1). We include a temperature-dependency in the maximum growth rates r_i of phytoplankton, the maximum

grazing rates G_j of herbivores, the clearance rate a_j of carnivores and the carnivore mortality rate m_j (mimicking fish grazing), as the metabolic activity of all these organisms is reduced at low temperatures. The temperature-dependent rates are given by

$$\psi(T) = \psi_{T_{max}} Q_{10}^{\frac{T - T_{max}}{10°C}} \tag{3}$$

with $\psi \in \{r_i, G_j, a_j, m_j\}$ and $\psi_{T_{max}}$ being the respective rate at the maximum temperature within the growing season. We assume that phytoplankton and small herbivores exhibit a lower temperature sensitivity than the large herbivores and all carnivores which are predominantly crustaceans. Crustaceans are known to have a more strongly reduced performance at low temperature (Sommer et al. 2012) compared to unicellular organisms which corresponds to a higher Q_{10} (Table 1). Fishes are also very sensitive to low temperature. Thus, we assume

also a high Q_{10} for the carnivore mortality rate m_j caused by fish (Table 1).

Results

The observed biomass and trait dynamics of phytoplankton, herbivorous and carnivorous zooplankton exhibit a pronounced seasonal succession and are highly repetitive among years (Fig. 3a–c). Rapid changes in biomasses and traits of all three trophic levels are interrelated and occur especially during spring and summer. In contrast to preliminary considerations (Fig. 1), the herbivore size (i.e., counter-defense) increases prior to the increase of phytoplankton defense, which then goes along with a simultaneous shift in carnivore size (Fig. 3b,c). The food web model reproduces the observed

dynamics and demonstrates that group-specific predation of carnivores may cause this reversed order of trait changes (Figs. 3d–f, 4). In the following, we first describe the observed biomass and trait dynamics. Subsequently, we link these patterns to our model results and present insights on mechanisms driving the order of trait changes.

Observations
Biomass dynamics

Starting from low biomasses at the beginning of the growing season, both phytoplankton and herbivore biomass strongly increase between week −12 and −6, i.e., 12 and 6 weeks before the clear-water phase (Fig. 3a). At the same time, the carnivores only slightly increase in biomass (Fig. 3a).
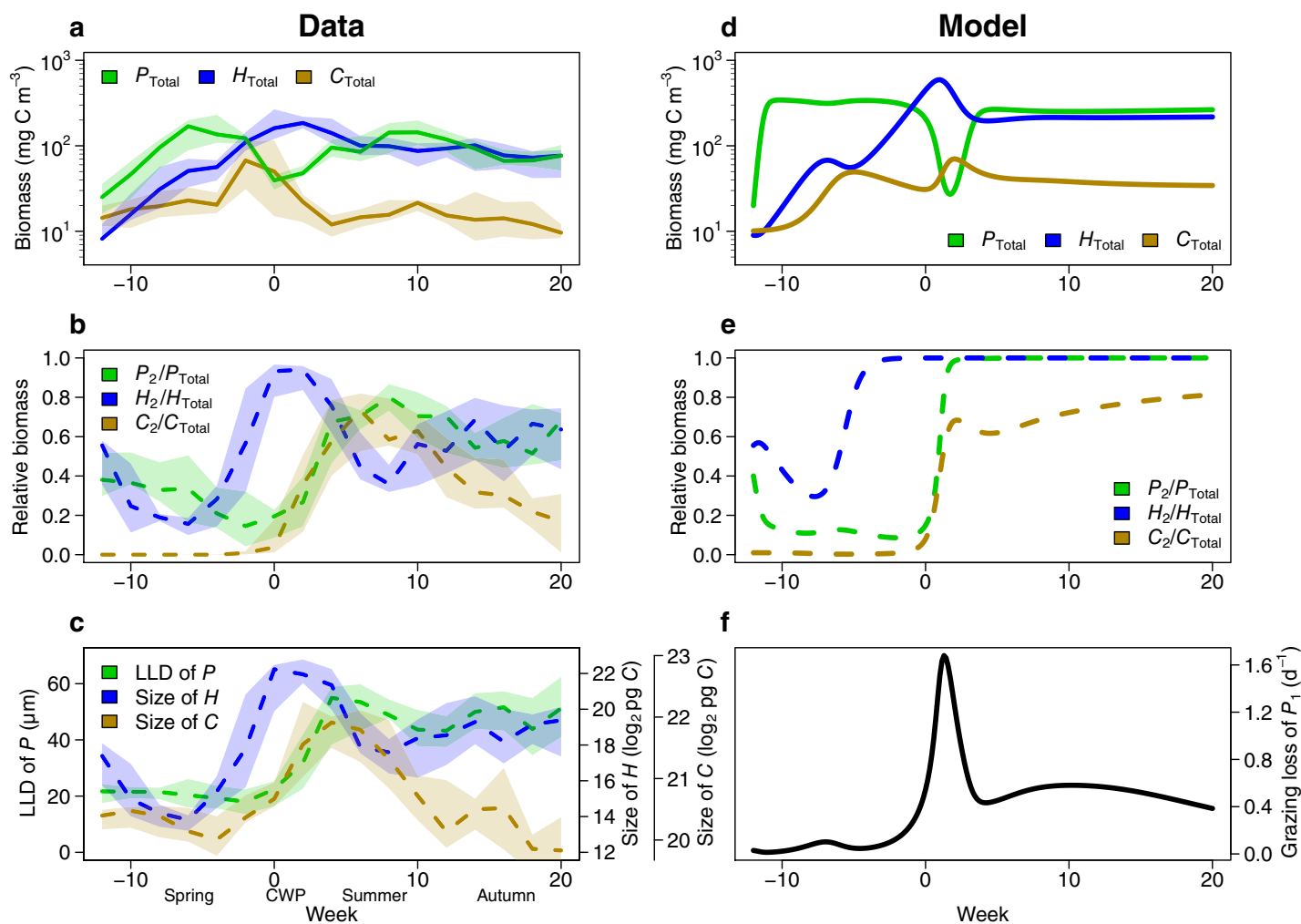

Fig. 3. Observed and simulated biomass and trait dynamics. (**a–c**) The data represent interannual medians from 1987 to 1996 in a biweekly resolution where the time dimension is scaled relative to the onset of the clear-water phase (CWP, week 0, approximately at end of May or beginning of June). The shaded areas around the lines display the respective interquartile ranges (median ± 25%). The trait dynamics of the three trophic levels are displayed either (**b**) by the relative contribution of functional groups or (**c**) by the mean trait values. (**d**) Numerical simulations of biomass and (**e**) trait dynamics for the standard parameter set. Panel (**f**) displays the grazing-induced mortality rate of well-edible phytoplankton P_1. The increase of this grazing loss coincides with the increase of phytoplankton defense (P_2/P_{Total}). P_{Total} denotes the total phytoplankton biomass, H_{Total} the total herbivore biomass and C_{Total} the total carnivore biomass. Biomasses of less-edible phytoplankton, large herbivores and large carnivores are given by P_2, H_2, and C_2, respectively.
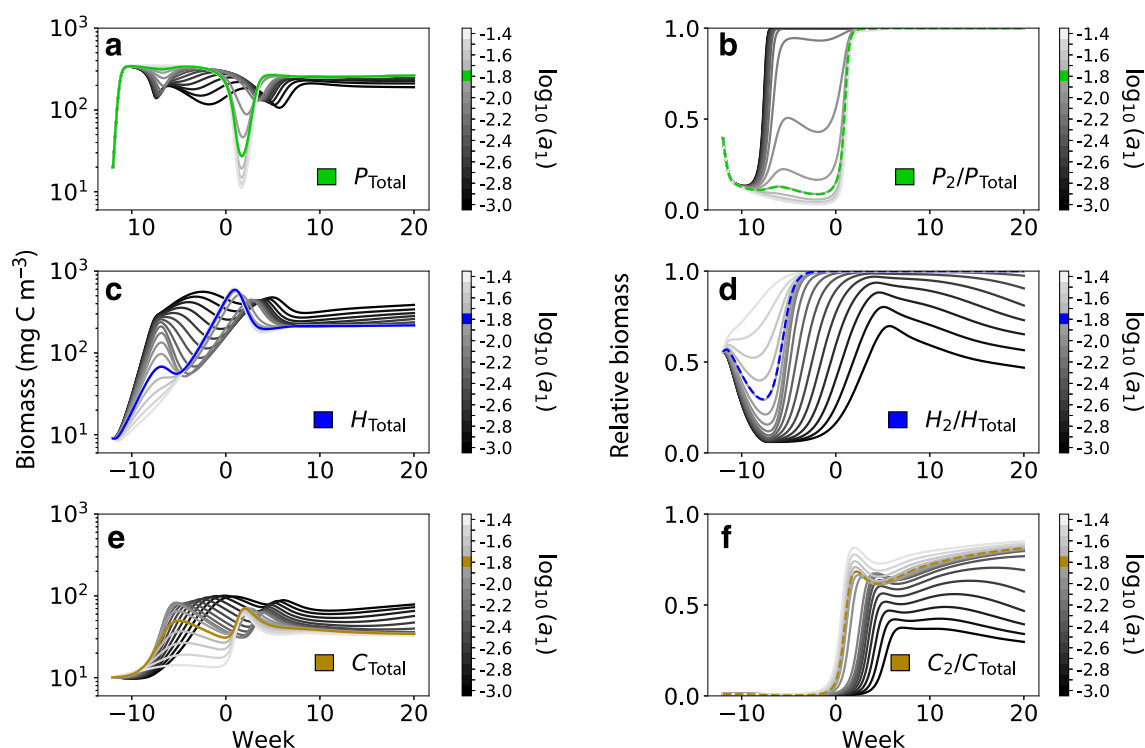
Fig. 4. Sensitivity of biomass and trait dynamics of (**a** and **b**) phytoplankton, (**c** and **d**) herbivores and (**e** and **f**) carnivores to a varied clearance rate of small carnivores (a_1) within the range of literature values. The grayish-black lines represent numerical simulations for the different values of a_1, in steps of $10^{0.1}$ $d^{-1}(mg\ C\ m^{-3})^{-1}$ displayed at the bar. Colored lines refer to the standard parametrization used before (i.e., $a_1 = 0.016$ $d^{-1}(mg\ C\ m^{-3})^{-1} \approx 10^{-1.8}$ $d^{-1}(mg\ C\ m^{-3})^{-1}$).

Around week −6, the phytoplankton biomass reaches a maximum, corresponding to the spring bloom (169 mg C m^{-3}), while herbivore biomass continues to increase (Fig. 3a). In early summer around week 0, the high herbivore biomass (185 mg C m^{-3}) causes a strong decrease and a distinct minimum of phytoplankton biomass (39 mg C m^{-3}), the so-called clear-water phase (CWP) (Fig. 3a). The carnivore biomass peaks prior to the CWP (67 mg C m^{-3}). After the CWP, the phytoplankton recovers and builds up a summer bloom around week 8 (144 mg C m^{-3}), while herbivore and carnivore biomasses are declining (Fig. 3a). Similar to the spring bloom, the summer bloom of phytoplankton is then followed by a slight increase and a peak of herbivore biomass. In general, the biomasses of all three trophic levels show a lower variability and level off at the end of the growing season (Fig. 3a).

Trait dynamics

Shifts in the relative biomasses of functional groups imply changes in the mean trait values of the trophic levels; for example, an increasing amount of less-edible algae corresponds to an increasing mean longest linear dimension (LLD) of phytoplankton (Fig. 2). These two measures of the trait dynamics are in very good agreement for all three trophic levels (Fig. 3b,c). Minor deviations between them arise from

intra-group variation (e.g., different less-edible phytoplankton species vary in their LLD) and additional classification criteria of the functional groups (e.g., the shape of phytoplankton cells). In the following, we use mainly the relative biomasses of the functional groups to describe the trait dynamics, being directly comparable with the model results.

During spring, the phytoplankton community is increasingly dominated by fast-growing, well-edible species. The herbivore community is initially driven towards fast-grazing, small species (mostly ciliates), being the preferred prey of small carnivores (cyclopoid copepods) (Fig. 2) which highly dominate the third trophic level at that time (Fig. 3b). Around week −6, the mean size of the herbivores starts to rapidly increase (more herbivorous cladocerans) during the phytoplankton spring bloom consisting mainly of well-edible algae. The contribution of large herbivores, such as daphnids, increases from 16% to 93% (Fig. 3b,c). Subsequently, with the onset of the CWP (week 0), the amount of slowly growing less-edible species in the phytoplankton community strongly increases from 19% to 80% (Fig. 3b,c). Simultaneously, the composition of the carnivore community shifts towards larger species (carnivorous cladocerans) from nearly 0–73% (Fig. 3b), which consume large herbivores (Fig. 2). In the further course of the growing season, the phytoplankton is dominated by

less-edible species, while herbivore size first declines and then increases after the phytoplankton summer bloom (Fig. 3b). The contribution of large carnivores continuously decreases from week 6 onwards until the end of the growing season (Fig. 3b).

Food web model
Simulated biomass and trait dynamics

The simulated biomass and trait dynamics are generally in good agreement with the empirical data, especially during spring and early summer (Fig. 3a,b,d,e). The model qualitatively reproduces the phytoplankton spring bloom during which the herbivore size (i.e., counter-defense for phytoplankton) rapidly increases after an initial decline. This shift in the herbivore community coincides with a peak of small carnivores, i.e., high C_{Total} and low C_2/C_{Total} (Fig. 3a,b,d,e), which preferentially feed on small herbivores (Fig. 2). The phytoplankton is well-edible at that time (low P_2/P_{Total}), suggesting that the increase of herbivore size is driven by the grazing impact of small carnivores rather than phytoplankton defense.

Similar to the data, simultaneous rapid increases of phytoplankton defense and carnivore size occur after that of herbivore size around the CWP, where herbivore biomass is maximal and phytoplankton biomass reaches a minimum (Fig. 3a,b,d,e). The model reveals that the grazing losses of well-edible phytoplankton are maximal at that time (Fig. 3f), driving the selection for phytoplankton defense (Fig. 3e). These grazing losses depend on the weight-specific grazing rates and the biomasses of the herbivores (Eq. 1). During the CWP, the high biomasses of large herbivores (Fig. 3d,e) compensate for their lower weight-specific grazing rates compared to small herbivores (Fig. 2) and impose maximal grazing losses on well-edible phytoplankton (Fig. 3f). This favors less-edible phytoplankton (Fig. 3e), even if it is partly consumed by large, counter-defended herbivores (Fig. 2). As observed, the modeled herbivore biomass then decreases at the time of low phytoplankton biomass, increased phytoplankton defense and higher biomasses of large carnivores (Fig. 3a,b,d,e), which graze on large herbivores (Fig. 2).

After the formation of the summer algal bloom, the observed and simulated dynamics show slight differences. The model overestimates the relative biomasses of less-edible phytoplankton, large herbivores and large carnivores during summer and autumn (Fig. 3b,e).

Model sensitivity analysis—testing the mechanism driving the order of trait changes

Here, we examine the mechanism underlying the pattern that herbivore size, i.e., counter-defense, increases prior to the increase of phytoplankton defense (Fig. 3b,c,e), which is reversed compared to predictions from bitrophic systems (Fig. 1). In Fig. 4, we vary the clearance rate of small carnivores (a_1) in the model within the broad range of literature values

(see Table 1) to test whether this reversed order is caused by a top-down control of small herbivores during spring, preventing them from establishing a sufficiently high grazing pressure to induce trait changes in the phytoplankton. For other processes, which may restrict their biomass, see "Discussion" section.

Decreasing a_1 by up to a factor of 3, relative to the standard value, does not alter the order of trait changes. For even lower values of a_1, a more pronounced biomass peak of small herbivores occurs around week −7 (high H_{Total}, low H_2/H_{Total}) (Fig. 4c,d), due to the lower top-down control by carnivores, which hardly benefit from higher biomasses of their prey given their low a_1 (Fig. 4e). In contrast to the observed dynamics and model simulations with the standard parametrization (Fig. 3), this initiates a decrease of phytoplankton biomass and a rapid increase in the relative biomass of less-edible algae (i.e., defense) already during spring (Fig. 4a,b), before the shift in herbivore size (i.e., counter-defense) occurs (Fig. 4d). A strong decrease in a_1 delays the trait changes in herbivores and carnivores (Fig. 4d,f). Overall, at the lowest published clearance rates (e.g., $a_1 = 10^{-3.0}$), the trait shifts at the three trophic levels occur consecutively starting with the first trophic level (Fig. 4b,d,f), as predicted by previous theory (Fig. 1). A similar pattern occurs for initial biomasses of small carnivores below the observed values, mimicking a smaller winter population, which also reduces the top-down control of H_1 and already leads to an increase of phytoplankton defense during spring (Fig. S3).

Increasing a_1 does not alter the main pattern that herbivore counter-defense increases before phytoplankton defense and carnivore size, but modifies the extent and timing of trait changes (Fig. 4b,d,f). Especially, the herbivores increase earlier in their mean size given the high grazing pressure on small herbivores.

Discussion

Our results provide first empirical evidence for rapid mutual biomass–trait adjustments among three trophic levels in a natural food web, using a long-term plankton data set of Lake Constance. The observed patterns of biomass and trait dynamics were highly repetitive among years (Fig. 3a–c) and can be qualitatively reproduced by a simple food web model (Fig. 3d, e), which aggregates species into functional groups according to their trophic interactions (Fig. 2). The functional trait values of the different trophic levels changed in an unexpected order: herbivores first became larger (late spring), implying the possibility to handle defended prey but at the cost of a lower maximum grazing rate, before phytoplankton became more defended (early summer). We explained this counter-intuitive pattern by group-specific predation of the third trophic level (Fig. 4), driving a "trophic biomass–trait cascade." High biomasses of small carnivores (cyclopoid copepods) exert a top-down control on small herbivores (ciliates

and rotifers) during spring. This obviated the need for phytoplankton to defend until the herbivores increased in size, reducing herbivore grazing losses by small carnivores. The resulting very high biomasses of large herbivores (mainly daphnids) during early summer imposed a high grazing pressure on phytoplankton (Fig. 3f) and made the algal defense then profitable, despite the lower weight-specific grazing rates of large herbivores compared to small herbivores and despite the fact that large herbivores graze somewhat also on defended algae. Hence, our results highlight that the understanding of trait dynamics in natural food webs demands insights on the interplay between traits and biomasses across multiple trophic levels.

Cyclopoid copepods, i.e., the small carnivores, are able to strongly graze on small herbivorous ciliates as they prevail in Lake Constance (Wickham 1995; Adrian and Schneider-Olt 1999) and can exert a strong top-down control on them during spring (Hansen 2000). Crucial for the suppression of small herbivores during spring, causing the reversed order of predator–prey trait adjustment, are the early spring biomasses of cyclopoid copepods (overwintering strategy) and their grazing performance (clearance rate), among other processes discussed below. The dominant cyclopoid copepod during spring, *Cyclops vicinus*, terminates its diapause during winter and reaches high biomasses already in March (Seebens et al. 2009, 2013), allowing for a high grazing impact on ciliates. The copepods are generally present at higher biomasses at the beginning of the growing season compared to other crustaceans in this lake. For example, the large carnivorous cladocerans *Bythotrephes* and *Leptodora* are absent in the plankton during winter and early spring (Straile and Hälbich 2000), and herbivorous daphnids either poorly overwinter as adults or hatch from ephippia during spring (George and Hewitt 1999; Sommer et al. 2012). Our model sensitivity analysis underlines that the observed biomasses of cyclopoids in early spring are sufficient for the top-down control of ciliates (Fig. S3). Strongly decreasing the initial cyclopoid biomasses, compared to observations, would mitigate ciliate mortality and would enable higher ciliate feeding on phytoplankton, potentially leading to an early spring increase of phytoplankton defense (Fig. S3).

The clearance rate value used in our model lies at the upper half of the broad range found in the literature for *C. vicinus* (*see* Table 1) feeding on different species of rotifers (Santer 1993; Plaβmann et al. 1997) or ciliates (Hansen 2000). Our model reveals that decreasing the clearance rate to the lower half of that range alters the trait dynamics, that is, phytoplankton defense increases before herbivore size (Fig. 4). Hence, depending on the parametrization, modeling studies may end up with different conclusions on the degree of top-down control of small herbivores by cyclopoids during spring (Kerimoglu et al. 2014). However, Hansen (2000) showed empirically even for clearance rates at the lower limit of this range, that cyclopoid copepods can strongly top-down control

ciliates in a small, eutrophic lake during spring. This is potentially linked to the fact that lab measurements of copepod clearance rates often underestimate the clearance rates realized in nature, where food is heterogeneously distributed in space, in contrast to lab conditions. The alternation between patches with and without food is beneficial to copepods (Dagg 1977) and allows for higher clearance rates, compared to a continuous food supply (Tiselius 1998). Indeed, the relative high production to biomass ratios of small herbivores during spring in Lake Constance (Gaedke et al. 2002) indicate high losses by copepod predation, which in turn likely reduces the grazing impact of small herbivores on phytoplankton. When released from top-down control, very high ciliate concentrations can promote a shift towards large and defended phytoplankton species, as observed in a small, eutrophic lake with very low crustacean abundance due to heavy fish predation (Lischke et al. 2016). Therefore, we argue that the top-down control of ciliates is a plausible reason for the dominance of undefended phytoplankton during spring at favorable light and nutrient conditions.

In addition to strong grazing by small carnivores, further potential explanations for the damped biomasses of small herbivores in spring include: (1) Intra-guild predation: large herbivores (*Daphnia* and *Eudiaptomus*) are able to prey also on small ciliates, which was not implemented in the model, but may contribute to the dampening of small herbivore growth (Wickham and Gilbert 1991; Adrian and Schneider-Olt 1999). (2) Interference competition: ciliates and rotifers can be damaged by filter-feeding Daphnia when getting into their branchial chamber (Gilbert 1989; Wickham and Gilbert 1991). (3) Mutual intra-group adaptation within well-edible phytoplankton and ciliates may stabilize the biomass dynamics in spring, preventing high peaks in ciliate biomasses and strong declines in well-edible phytoplankton (Tirok and Gaedke 2007, 2010). Independent of which of these mechanisms may dominate, we argue that small herbivores bear an additional cost for their high grazing rates, that is, not only in respect to their reduced prey spectrum but also an ecological cost, emerging in the presence of predators, competitors or adaptation in prey (van Velzen and Etienne 2015).

External forcing by abiotic factors (e.g., irradiance, temperature, vertical mixing) plays an important role for the plankton dynamics in winter and determines the onset of phytoplankton growth in early spring, but it is of minor importance during the studied growing season when the lake is stratified (Sommer et al. 2012). Thus, we argue that the observed trait dynamics are primarily endogenously driven by competition and trophic interactions, and that the general patterns are quite robust against weather conditions. For example, excluding the implemented temperature sensitivity of the growth and grazing rates in the model does not alter the overall order of trait changes (Fig. S2). It only decreases the quantitative fit to the data, that is, the main changes in biomasses and traits start too early in the growing season (Fig. S2). Nevertheless,

nutrients play a key role for the plankton dynamics during the growing season. However, they are not considered as a purely exogenous driver here, given the small vertical and horizontal nutrient inputs into the euphotic zone in this large, deep lake during stratification. Hence, the nutrient dynamics in the relevant strata are directly linked to the biomass dynamics and trophic interactions, i.e., endogenous processes, in this lake during the growing season.

The model captured the major characteristics of the observed biomass and trait dynamics well during spring and early summer, but overestimated the relative biomasses of less-edible algae, large herbivores and large carnivores from midsummer onwards. This implies that processes, which select towards the opposite trait directions (i.e., high edibility of algae, small size of herbivores and carnivores), are then not sufficiently accounted for in the model. The following processes may be relevant: (1) sedimentation causes an additional background mortality during summer stratification especially to numerous of the less-edible phytoplankton species, e.g., large diatoms (Sommer 1984). (2) Parasites (e.g., chytrid fungi) may infect especially less-edible phytoplankton at higher temperatures mitigating summer blooms (van Donk and Ringelberg 1983; Sommer et al. 2012). Adverse effects of parasites have been observed also for daphnids, i.e., reducing the biomass of large herbivores (Bittner et al. 2002). (3) Diapause of small carnivores (*C. vicinus*) during summer contributes to the observed decline of carnivores (Seebens et al. 2009), not reflected by the model, and releases small herbivores from strong grazing pressure, and thus may explain their higher observed biomasses. (4) Fish predation, especially on large carnivores (*Bythotrephes* and *Leptodora*) but also on large herbivores (*Daphnia*), is at its maximum during summer and very likely contributes to the decrease of mean carnivore and herbivore size at this time (Luecke et al. 1990; Straile and Hälbich 2000).

We did not further resolve the impact of fish larvae and fish acting at the third and fourth trophic level in the data analysis and our model for several reasons: (1) The planktivorous fish is under very heavy fishing pressure. (2) In such a large and deep lake, little benthic food subsidies do not promote a maintenance of high fish grazing pressure on zooplankton (Jeppesen et al. 1997). (3) Fish larvae are extremely heterogeneously distributed, making it impossible to assess their abundance reliably. (4) Carnivorous zooplankton is the major consumer of herbivorous zooplankton (Gaedke and Straile 1994). Hence, our model with its simple structure considering the trophic interactions among six fixed functional groups at three planktonic trophic levels is an appropriate approximation. It reproduces the most striking patterns in the biomass and trait data, and its low complexity allows us to detect the reason why it reproduces the observed order of trait changes and to examine conditions reversing it (Fig. 4).

Changes in the functional composition of one trophic level may have cascading effects on the functional composition of adjacent trophic levels (Carpenter et al. 1985; Leibold et al. 1997). Kenitz et al. (2017) were the first to describe such interactions among trophic levels as a "trophic trait cascade." They considered two trophic levels, marine copepods feeding on protists, and found that the upper trophic level adjusted its feeding type in response to preceding changes in motility of the lower trophic level. In contrast, we found trait changes at the second trophic level which did not arise from adjustment to the trait composition of the first trophic level, but were driven by the third one. Furthermore, we observed trait changes within the first trophic level (increase of defense) which do not match the altered herbivore trait composition (increased counter-defense). The increased defense of phytoplankton was likely caused by the higher biomass rather than the altered trait composition of herbivores, which escaped from carnivore predation by getting larger. This leads us to the concept of "trophic biomass–trait cascades": both biomass and trait changes can cascade through trophic levels and mutually affect each other, where trait alteration at one trophic level can be driven either by changes in traits or biomasses of adjacent trophic levels. We consider our concept as a generalization of that of "trait-mediated indirect effects" (Werner and Peacor 2003; Schmitz et al. 2004), where the trait composition of an intermediate tropic level changes in response to enhanced biomasses of a higher trophic level, which alters the biomass of the bottom trophic level. Our results provide empirical evidence for a "trophic biomass–trait cascade" in a natural food web. Importantly, the changes in traits and biomasses can feedback on each other.

We conclude that, in multitrophic food webs, traits of trophic levels can be altered in an unintuitive way by underlying and overlying trophic levels. This challenges the predictive power and applicability of models classically ignoring or considering trait adjustment of only one or two trophic levels. In our study, the interaction of traits and biomasses among three trophic levels led to a reversed order of trait changes, being impossible to understand with a bitrophic view. Such reversed trait dynamics probably emerge in many natural food webs and may lead to misleading conclusions on the underlying mechanisms. This asks for multitrophic, trait-based approaches enhancing the understandability and predictability of trait changes in nature.

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Conflict of Interest

None declared.