Prey density drives diet shift of the invasive mysid shrimp, Limnomysis benedeni

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Abstract

Understanding the diet preferences and prey selection of invasive species is crucial to better predict their impact on community structure and ecosystem functioning. Limnomysis benedeni, a Ponto-Caspian invasive mysid shrimp, is one of the most successful invaders in numerous European river and lake ecosystems. While existing studies suggest potentially strong trophic impact due to high predation pressure on invaded plankton communities, little is known of its prey selectivity between phyto- and zooplankton, under different prey concentrations. Here, we therefore investigated the feeding selectivity of L. benedeni on two commonly occurring prey organisms in freshwaters, the small rotifer zooplankton Brachionus calyciflorus together with the microphytoplankton Cryptomonas sp. present in increasing densities. Our results demonstrated a clear shift in diet selection, with L. benedeni switching from B. calyciflorus to Cryptomonas sp. already when the two prey species were provided in equal biomasses. Different functional responses were observed for each prey type, indicating somewhat different foraging mechanisms for each prey type. These findings provide experimental evidence on the feeding flexibility of invasive mysid shrimps and potential implications for trophic interactions in invaded ecosystems.

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Abstract

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the microphytoplankton *Cryptomonas* sp. present in increasing densities. Our results demonstrated a clear shift in diet selection, with *L. beneden* i switching from *B. calyciflorus* to*Cryptomonas* sp. already when the two prey species were provided in equal biomasses. Different functional responses were observed for each prey type, indicating somewhat different foraging mechanisms for each prey type. These findings provide experimental evidence on the feeding flexibility of invasive mysid shrimps and potential implications for trophic interactions in invaded ecosystems.

Keywords: *Limnomysis benedeni* , prey density-dependent foraging, diet shift, invasive species, prey selectivity

Introduction

Diet shift and prey selectivity are among the most important aspects to understand the impact of a predator on community structure and food web functioning (Greene, 1983; Sailley et al., 2015). Prey selection is influenced by multiple variables such as the predator's ontogenetic stage, prey availability and size, and environmental factors such as temperature (Divoky et al., 2021; Graeb et al., 2006; Greene, 1986). According to the optimal foraging theory, the diet preference of an animal is influenced by maximizing net energy gain and minimizing the cost of obtaining the prey (Gooding & Harley, 2015, Krebs et al., 1977). At the same time, foraging behaviour can be adjusted in response to changes in prey density (Murdoch & Oaten, 1975). Usually, predators choose habitat patches with high prey availability as it can increase the chances of successful predation events (Ioannou et al., 2009; Wellenreuther & Connell, 2002). Besides quantity, diet preference can be also influenced by the nutritional quality of their prey (Mayntz et al., 2005; Schmidt et al., 2012). Along this trade-off, consuming smaller and less nutritious prey may only be beneficial if it is present in large quantities and/or if the higher quality prey is difficult to capture (Langerhans et al., 2021). Omnivores can show higher foraging flexibility and may switch between different diet items depending on their availability. Their ability to exploit more than one trophic level (Pimm & Lawton, 1978) allow them to affect the dynamics of an ecosystem through multiple pathways. Understanding the feeding behaviours of omnivores, especially invasive species, can provide insight into their functional roles, and be used to better predict population and ecosystem dynamics.

The spread of multiple Ponto-Caspian invaders in numerous European brackish and freshwater habitats and more recently in North American Great Lakes received considerable attention in the past decades (Bij de Vaate et al., 2002; Reid & Orlova, 2002; Ricciardi & MacIsaac, 2000). The invasion was initially facilitated via unintentional means such as migration through artificial canals, reservoirs acting as stepping stones on rivers, and passive transport by ships (Jażdżewski, 1980). The expansion was further supported by intentional introduction to improve the fish food resources (Karpevich, 1975). Crustaceans, specifically, amphipods, cladocerans, and mysids are among the most successful Ponto-Caspian invaders (Leppäkoski et al., 2002; Leppäkoski & Olenin, 2001; Ricciardi & Rasmussen, 1998). They can influence native communities by eliminating native species, decreasing functional diversity, and ultimately altering the energy flow in ecosystems (Dick & Platvoet, 2000; Jazdzewski et al., 2004; Ketelaars et al., 1999; Ojaveer et al., 2002).

Mysid shrimps, including species such as *Hemimysis anomala* ,*Limnomysis benedeni* , *Katamysis warpachowskyi* , and*Paramysis lacustris* , have become prominent Ponto-Caspian invaders. These species have successfully established in Europe (Audzijonyte et al., 2008, 2009; Borza et al., 2019; Wittmann, 2008), while *H. anomala* also invaded the North American Great Lakes (Audzijonyte et al., 2008). Traits such as wide environmental tolerance, omnivory, high annual number of generations, and related ability to get established quickly in new habitats likely contributed to their invasive success (Borza, 2014; Borza et al., 2017). Mysid shrimps are small, generally omnivorous crustaceans found in both marine and freshwater environments (Mauchline, 1980). They are grazers and predators of microorganisms and zooplankton (Viherluoto et al., 2000), and a primary food source for many fish species, birds, and other aquatic animals (Arrhenius & Hansson, 1993; Möllmann et al., 2004; Moran & Fishelson, 1971). They are facultative filter feeders, using their specialized thoracic limbs to filter plankton from the water column (Borza et al., 2023; Wittmann et al., 2014). By feeding on organisms from multiple trophic positions, and representing food for higher trophic levels, they occupy key positions in their ecosystems (Rakauskas, 2019). Therefore, their establishment and changes in abundance can have cascading effects on other organisms in the ecosystem (Kiljunen et al., 2020). To study the functional roles and impacts of invasive Ponto-Caspian mysid shrimps in invaded ecosystems, understanding their feeding interactions with native communities is therefore of high importance. Consequently, there are numerous studies exploring the feeding habits of native mysid shrimp species. For instance, omnivorous nature, role of predator and prey size, ontogenetic diet shift and seasonal migration to different aquatic zones have been explored (Arbačiauskas et al., 2013; Fink et al., 2012; Lesutienė et al., 2007; Penk & Minchin, 2014). However, limited data is available on the feeding ecology, specifically on the diet shift as a function of different prey types and densities in invasive Ponto-Caspian mysid shrimps.

Limnomysis benedeni is one of the most widespread omnivorous invasive mysids in continental Europe, including main river systems like the Danube, Rhine, neighbouring lakes and even some isolated lakes (Audzijonyte et al., 2009; Borza, 2014; Borza et al., 2011; Wittmann, 2007). *L. benedeni* feeds by actively selecting and capturing small-sized zooplankton, while also passively filtering smaller particles such as algal cells (Fink & Harrod, 2013). It can feed in both the benthic and pelagic zones which can affect the nutrient cycling in the littoral zone (Hanselmann et al., 2013). Earlier studies found that *L. benedeni* is a selective predator of zooplankton, and also suggested that prey density-dependent diet switching between phytoplankton and zooplankton may have a significant impact on plankton community structure and dynamics (Fink et al., 2012). However, the occurrence and direction of this diet shift were so far not quantified and studied in detail.

We aim to, through this study, yield a better understanding of the impact of phytoplankton and zooplankton density on the diet preference of *L. benedeni* . To do this, we compared the ingestion rates of *L. benedeni* on food mixtures containing a rotifer and a microalga, across increasing algal biomass. We expected the mysids to feed on the larger and highly nutritious zooplankters preferentially, and only switch to phytoplankton when present at sufficiently high biomass, which consequently reduces predation on rotifers.

Materials and Methods

Study organisms and culturing conditions

Two different types of prey, a microalga and a microzooplankton species, were used in the experiment. *Cryptomonas* sp. (strain 26.80 of the SAG Culture Collection, originally isolated from Lake Windemere, UK) was grown in WC medium (Guillard, 1975) enriched with Vitamin B12 (0.135 g L^{-1}) (recipe available at UTEX culture collection of algae, Texas website). The rotifer *Brachionus calyciflorus* (obtained from AQ4Aquaristics, Braunschweig, Germany) were cultivated in aerated and filtered (by a JBL Cristal Profi e702 external aquarium filter) tap water and were fed by *Cryptomonas* sp. Individuals of the mysid shrimp *Limnomysis benedeni* were collected from the littoral zone of Lake Balaton, Hungary, in March 2022 by a hand net. They were subsequently reared in lab aquaria at 20, under a 16:8 light: dark photoperiod, and gentle aeration. The population was fed with *Cryptomonas* sp. at saturating concentrations (>1 mg C L^{-1}) three times per week. Three-fourths of the volume (~3-4 litres) of the water in the aquaria was replaced with fresh filtered tap water twice a week.

Grazing experiment

In order to estimate the individual dry mass and carbon mass of *Cryptomonas* sp. and *B. calyciflorus* , we measured the axial dimensions of 20 randomly selected individuals of each species. The measurements were obtained using an inverted microscope (Zeiss Axio Vert.A1) after the individuals had been preserved with 10% Lugol's iodine solution. The biovolume of *Cryptomonas* sp. was approximated by using the formula for a prolate spheroid (Hillebrand et al., 1999). Afterwards, the carbon content of the algae was estimated using the formula $Cc\ (in\ pg/cell) = 0.109.\ V^{0.991}$ where V is the biovolume in µm^3(Weisse et al., 2001). The biovolume of the rotifers was estimated using the formula $Vr\ (in\ um^3) = \frac{4\Pi.l.w^2}{3}$ where l is the length (in µm) and w is the width of the rotifer (in µm) (Bottrell et al., 1976). The dry weight of the rotifers was calculated by assuming it to be 10% of the wet weight, which was calculated using the assumption that 1 mm^3 equals 1 mg (Pace & Orcutt Jr., 1981). The dry weight was then converted to carbon content using a conversion factor of 0.48 (Work et al., 2005).

Prior to the grazing experiment, *L. benedeni* specimens were pre-acclimatised to the experimental conditions (temperature and light) for 48 hours. We kept them in 200 ml glass jars with 160 ml of filtered tap water in two water baths at a constant temperature of 21, with gentle aeration and a 16:8 light and dark photoperiod. Each jar contained three individuals of *L. benedeni* , fed by a mixture of*Cryptomonas* sp. and *B. calyciflorus* at saturating densities (both at 1 mg C L^{-1}) during the first 24 hours, followed by exposing them to the experimental conditions (see below) in the next 24 hours. We applied a third water bath with the same treatments containing individuals of *L. benedeni* used as backup, in order to replace any dead individuals in the experimental jars to keep experimental biomass constant.

After this 48-hours pre-acclimatisation period, *L. benedeni*individuals were carefully rinsed in filtered tap water to remove any debris or food attached to them. To quantify grazing rates of *L. benedeni* on both prey types, we run a grazing experiment consisting of four treatment levels with different algae biomasses (corresponding to 0.1, 0.5, 1, and 1.5 mg C L^{-1}, ranging between ˜ 2,000k to 32,000k cells ml^{-1}), while rotifer biomass was kept constant (1 mg C L^{-1}, ˜ 3 rotifers ml^{-1}) across them. This setup was replicated four times. We applied two types of controls at each treatment levels: one containing only *Cryptomonas* sp. to measure the growth rate of algae (applied in two replicates) and the second containing both *Cryptomonas sp.* and *B. calyciflorus*to measure the consumption rate of algae by rotifers at different algae biomass treatments (applied in three replicates). The experiment was run for 14 hours under constant dim light (4000 K LED, overall light intensity approx. $3 * 10^{14}$ photons /cm^2/s). Other experimental conditions (i.e., medium, volume, temperature, aeration) were the same as described above for the pre-acclimatisation period. The few dead individuals (three) of *L. benedeni* were replaced with individuals from the backup cultures. At the end of the experiment, 1 ml and 10 ml samples were taken from each jar after thorough mixing to estimate the biomasses of*Cryptomonas* sp. and *B. calyciflorus* . The samples were fixed with Lugol's iodine solution and counting was done using a stereomicroscope (Zeiss Stemi 305) using a Sedgwick rafter cell counter (S50, Graticules Optics, UK) for *Cryptomonas* sp. and a Petri dish with grids for *B. calyciflorus* .

The specific growth rates, h^{-1} (k) of both prey types were calculated using formula suggested by Frost (1972):

$$k = \frac{ln(C2) - ln(C1)}{t2 - t1}$$

The grazing coefficients, h^{-1} (g) of *L. benedeni* were calculated by

$$g = kprey - \frac{[ln(C{*}2) - ln(C{*}1)]}{t2 - t1}$$

where C_1 and C_2 are initial and final prey abundances (algal cells or rotifer individuals mL^{-1}) in the control jars at timest_1 and t_2 andC^*_1 and C^*_2 are initial and final prey abundances (individuals mL^{-1}) in the jars with predators at times t_1 andt_2 . The mysid filtration and ingestion rates of mysids were calculated using formulae by Marin et al. (1986) and Nejstgaard et al. (2001).

Data analysis

We ran multiple models, including linear models, generalized linear models, and generalized additive models to test how different algal densities affect the ingestion rates of *L. benedeni* on*Cryptomonas sp.* and *B. calyciflorus* . Model selection was then based on the Akaike Information Criterion (AIC), which selected generalized additive models (GAM) to be the relative best-fit models (Burnham & Anderson, 2004). Ingestion rates on algae or rotifers were used as response variables, plotted against treatment levels (i.e., biomass of*Cryptomonas* sp.) respectively with k=4. We used the 'anova.gam' of the 'mgcv' R package to test the significance of the smooth term, treatment levels (Wood et al., 2016). Model assumptions (normality, heterogeneity of variances across treatments) were visually assessed via diagnostic plots (histogram of model residuals, residuals versus fitted values, normal Q-Q plots) and no deviations were found. All statistical tests were performed using R studio version 4.1.1 with nlme, mgcv, and ggplot2 packages (José Pinheiro et al., 2022; R Core Team, 2021; Wickham H, 2009; Wood et al., 2016). Besides, to quantify the preference of *L. benedeni* for different prey items with respect to their relative biomass, we calculated Ivlev's index (e_i) for each prey type across treatments (Ivlev, 1961; Jacobs, 1974). Here, a positive score indicates a preference for a particular food item while a negative score may indicate inaccessibility or avoidance of the food item (Jacobs, 1974). We also calculated and plotted the relative biomasses (mean of three replicates with 95% confidence intervals) ingested from each prey against their relative availability. Here any deviations from the 1:1 line indicate preferential feeding and a change in preference can be used to reveal prey switching (Cuthbert et al., 2018; Hughes & Croy, 1993).

Results

Ingestion rates of *L. benedeni* on *Cryptomonas* sp. increased in a slightly sigmoidal pattern with an increase in algae biomass (Fig. 1A). Parallel to this, ingestion rates on *B. calyciflorus* decreased following a clear sigmoidal pattern, with an abrupt decline occurring between the algae concentrations 0.5 and 1.0 mg C L^{-1} (Fig. 1A). The models explained 99.8% (adj. $R^2 = 0.998$) and 97.8% (adj. $R^2 = 0.978$) variance for algae and rotifer consumption as a function of algae biomass. Consumption of *Cryptomonas* sp. or *B. calyciflorus*by mysids were found to have a strong association with the experimental treatment levels (edf= 2.977 (for algae), p<0.001, edf= 2.948 (for rotifers), p <0.001). The total carbon biomass ingestion rate (i.e., the sum of ingested *Cryptomonas* sp. and *B. calyciflorus* carbon biomass) by *L. benedeni* increased with an increase in algae biomass. The relationship was non-linear, with a steeper increase above 1 mg C L^{-1} than below (Fig. 1B).

The Ivlev's electivity index suggested a treatment-specific (i.g. algae biomass dependent) preference for *Cryptomonas* sp. and *B. calyciflorous* (e_i>0). At lower algae biomass (0.1 mg C L^{-1} and 0.5 mg C L^{-1}), index values showed a preference for *B. calyciflorus* (e_i = 0.02 and 0.08) vs *Cryptomonas*sp. (e_i = -0.09 to -0.6). However, at higher algae biomass (1 mg C L^{-1} and 1.5 mg C L^{-1}) the pattern shifted to the opposite, with higher e_i values for *Cryptomonas* sp. (0.18 to 0.25) than for *B. calyciflorous* (ranging from -0.2 to -0.9).

The pattern of the relative contribution of *Cryptomonas* sp. and*B. calyciflorus* biomass to the total ingested biomass also confirmed treatment-specific preferential feeding. When rotifers were present in higher biomass than algae (i.e., 90.1% and 66.7% of total available biomass), their share in the ingested biomass was higher than could be expected in the case of non-preferential feeding, while lower in treatments with equal to or higher biomasses of *Cryptomonas*sp. Consequently, the pattern found for *Cryptomonas* sp. was similar, but mirrored (Fig. 2).

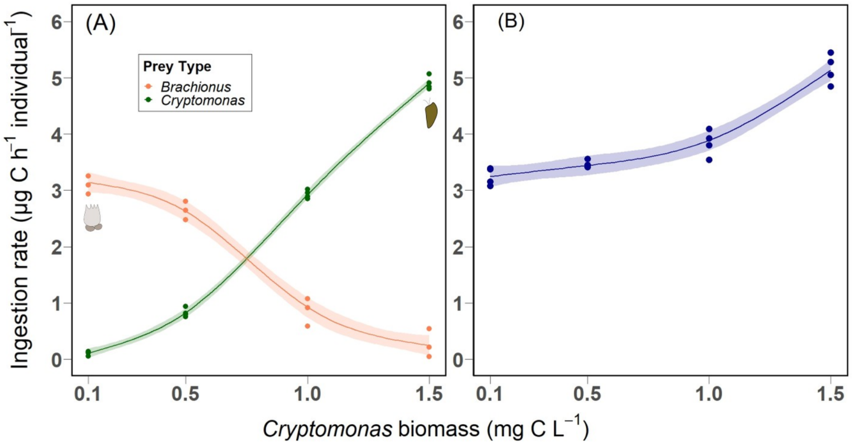

Figure 1: *Limnomysis benedeni* (A) ingestion rates (µg C h^{-1}) on *Cryptomonas* sp. (dark green) and*B. calyciflorus* (orange) across treatments (i.e., increasing initial biomass of *Cryptomonas* sp.). Solid lines represent fitted generalized additive models with coloured bands representing 95% confidence intervals. (B) Total ingested plankton biomass (sum of ingested *Cryptomonas* sp. and *B. calyciflorus* carbon biomasses, µg C L^{-1}) with the increasing original biomass of *Cryptomonas* sp.

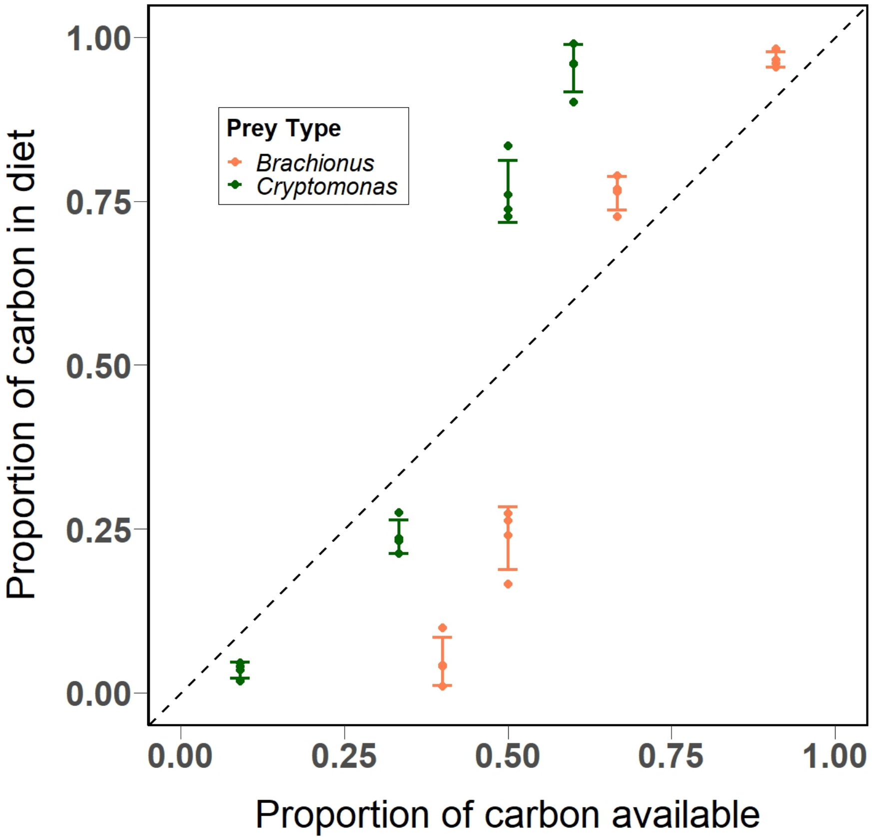

Figure 2: Relative contribution of prey carbon biomass to the total ingested biomass by *Limnomysis benedeni* plotted as a function of the relative contribution of each prey to total available carbon biomass. Prey types used are *Cryptomonas* sp. (dark green) and*B. calyciflorus* (orange). Solid dots represent samples while error bars indicate the 95% confidence intervals. The dashed 1:1 line represents where *L. benedeni* would be consuming a prey proportional to its availability, meaning random food uptake (neither preference, nor avoidance).

Discussion

Our results clearly showed that the diet preference of *L. benedeni* depends on the relative (C) biomass concentration of prey types, by shifting from microzooplankton to phytoplankton prey with increasing phytoplankton prey biomass. The patterns of consumption rates in response to relative prey biomass differed between the prey types suggesting slightly different functional responses for the microzooplankton and phytoplankton prey. While both resembled a sigmoidal pattern (Fig. 1A), the ingestion rate on *B. calyciflorus* followed a type III functional response more clearly, which usually indicates either prey switching or efforts to modify foraging behaviour in response to the prey density (Holling, 1959; Kiørboe et al., 2018; Thomas et al., 1996). In the case of*Cryptomonas* sp. after a slower increase at low densities, the pattern was closer to linear and did not show saturation within the tested biomass range during the experiment, overall resembling a type I functional response (Holling, 1959), suggesting that consumption of *Cryptomonas* sp. is primarily a function of density.

The decreasing consumption rates on rotifers with increasing algae concentration illustrated how the presence of alternative prey items in sufficient densities can lead to decreased predation pressure on another type of prey. If more than one alternative food source is present, predators can select based on prey-specific encounter rates to optimize foraging time and energy intake (Krebs et al., 1977). Specifically, the relative attack rate is a function of relative density and the switching can happen only if the likelihood of attacking the last eaten species is higher than attacking other species (Oaten & Murdoch, 1975). In our case, the cost-to-benefit ratio changes in favour of algae at higher algae densities. Indeed, we found that algae consumption increased in comparison to rotifer consumption for biomass equal to or higher than 1 mgC L^{-1}. This is also supported by Ivlev's index results which point towards the flexibility in the feeding behaviour of *L. benedeni* depending on algal density. The Ivlev's indices indicate a preference for rotifers in the presence of low algae biomass and avoidance of algae and vice versa with high algal biomass.

Predators typically select their diet based on size, nutritional quality, and escape responses of the prey (Cotonnec et al., 2001; Frost, 1972; Viitasalo & Rautio, 1998). They would try to increase their fitness by acquiring prey with easier access and lower cost-to-benefit ratio (MacArthur & Pianka, 1966; Pyke et al., 1977; Stephens & Krebs, 1986). Earlier studies suggest that *L. benedeni* is not an optically-oriented predator but selects its food based on size (Fink et al., 2012). Here we provided *L. benedeni* with two types of food with very different sizes. Purely from a size-based perspective, feeding on the smaller prey is only beneficial when available in sufficient densities, which was indeed confirmed by our results, with *L. benedeni*showing a gradual shift to the smaller prey with its increasing quantity.

Prey nutritional quality can also affect the development of consumers and influence their dietary choices (Gulati & Demott, 1997; Meunier et al., 2016). For instance, algae generally have a higher carbon-to-nutrient ratio than animal prey (Elser et al., 2000; Sterner & Hessen, 1994). In the case of *Cryptomonas* SAG 26.80, a C:P ratio of ~150 and a C:N ratio of ~22 were reported during the exponential growth phase (i.e. when nutrients are not limiting growth; Vad et al., 2020). For *B. calyciflorus* , C:P ratios are relatively constant around ~92, while C:N are ~4 (Jensen & Verschoor, 2004), which is very close to the body stoichiometry of omnivorous crustaceans such as mysids (C:P~90 and C:N ~4) (Arbačiauskas et al., 2013). Therefore, based on a purely elemental stoichiometric point of view (Laspoumaderes et al., 2010), rotifers would be the preferred prey. The higher C to nutrient ratios of algae may explain the pattern we found in the case of total ingested carbon biomass, which instead of steadily increasing showed an accelerating increase at the highest *Cryptomonas* sp. biomass level. This may indicate that *L. benedeni* needs to increase overall food uptake when feeding on algae, to obtain sufficient amounts of nutrients.

Other factors such as essential fatty acids (Ahlgren et al., 1990; Brett & Müller-Navarra, 1997; Ramlee et al., 2021; Trommer et al., 2019), or vitamins (Fridolfsson et al., 2018, 2019; Hessen, 1992) can also influence food quality.*Cryptomonas* sp. is considered to be a high-quality algal food source based on the high cellular content of essential fatty acids (Von Elert & Stampfl, 2000; Weers & Gulati, 1997). Consequently, the results may differ if the autotrophic food quality is less cost-efficient for the predator than the heterotrophic prey. For instance, had a 'less favourable' algal food source, such as green algae, been used, the preference for rotifers might have been more pronounced. Nonetheless, a preference for green algae (*Chlamydomonas sp.*) over zooplankton has been observed previously at an algal biomass of 0.3 mg POC L^{-1} as well (Fink et al., 2012).

Given that our study is based on a short-term experiment, there are some aspects in which its results might differ from patterns arising in natural communities. For instance, the container size in laboratory studies is a factor that may influence predator behaviour (Bergström & Englund, 2004; Toonen & Fu-Shiang, 1993). Therefore, a small-sized jar could have increased the competition among mysids thus forcing them to choose algae, a 'costly prey', to consume maximum food to maintain their energy budget. In addition, in this grazing experiment, we did not include predators of mysids, though in natural ecosystems optimal foraging strategy is based on a tradeoff between nutritional needs and simultaneously minimising the risk of predation as described in the unified foraging theories (e.g., Mangel & Clark, 1986). Experiments with another trophic level (e.g., small fish), carried out in larger mesocosms, could therefore provide more specific predictions on these tradeoffs in the future, including longer-term effects on ecosystem stability.

Despite these limitations, our results provide important implications for plankton community dynamics in natural ecosystems. Depending on the relative biomasses of phyto- and zooplankton, mysid shrimps may act as predators or competitors of zooplankton, being intraguild predators of the latter. By always suppressing the more abundant planktonic prey, they may reduce the amplitude of predator-prey oscillations, thereby contributing to ecosystem stability. However, there are certainly other possible scenarios as well, as illustrated by the effects of other invasive omnivorous Ponto-Caspian mysids. For example, *Hemimysis anomala* and *Paramysis lacustris* were both found to contribute to the alteration of trophic pathways in their invaded habitats, due to their strong predatory impact on zooplankton and benthic macroinvertebrate communities (Evans et al., 2018; Ketelaars et al., 1999; Rakauskas, 2019). For a better understanding of the potential effects of omnivorous mysids on trophic cascades and food web stability, studying their feeding mechanisms and diet selection is of high importance. Field observations coupled with laboratory and mesocosms studies could contribute to understanding the mechanisms underlying community and ecosystem-level effects of these widespread (and still spreading) invasive species.

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Author's contributions

- Varsha Rani- Conceptualization (Equal), Methodology (Equal), Data curation (Lead), Formal analysis (Equal), Original draft of the paper (Lead), Revision of the paper (Equal)
- Zsófia Horváth- Conceptualization (Supporting), Formal analysis (Equal), Revision of paper (Equal), Supervision (Supporting)
- Jens C. Nejstgaard- Conceptualization (Equal), Methodology (Supporting), Revision of the paper (Equal)
- Ádám Fierpasz- Methodology (Supporting), Revision of the paper (Supporting)
- Károly Pálffy- Formal analysis (Equal), Revision of the paper (Equal)
- Csaba F. Vad- Conceptualization (Equal), Methodology (Equal), Resource (Lead), Data curation (supporting), Formal analysis (Equal), Original draft of the paper (Lead), Revision of the paper (Equal), Supervision (Lead), Funding acquisition (Lead)

Conflict of Interest Statement

The authors declare no conflict of interest.

Data availability statement

The data used to draw graphs in the study is available on Dryad https://datadryad.org/stash/share/xURDH3d1npo2cOZhJ0oOr3EIF5Lxc2p1u2d0Zf1YE0w .

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