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Towards a mechanistic understanding of individual-level functional responses: Invasive crayfish as model organisms

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Abstract

- 1. In novel communities, a rising number of new and emerging invasive species interact with resident species, some of which are non-native themselves. We implemented an innovative trophic interaction framework for novel communities and quantified the interaction strength and impact potential of a truly novel species (marbled crayfish Procambarus virginalis) with a resident non-native counterpart (spiny-cheek crayfish Faxonius limosus). As prey, we used Dreissena mussels, which are non-native as well and now hold a key position in many European and North American aquatic ecosystems.
- 2. For both crayfish species, we predicted functional responses based on a mechanistic model that we parameterised with a set of experimental observations of foraging behaviour and satiation. We compared these predicted functional responses to empirically observed responses. In addition, we incorporated behavioural traits such as aggression, activity, and boldness in the comparisons between the species and individuals to determine their influence on functional responses. We tested individuals from aquarium stocks as well as naturalised individuals from invaded water bodies.
- 3. Altogether, we performed 1,095 experiments with 26 individual crayfish. We found that per capita predation of spiny-cheek crayfish exceeded that of marbled crayfish from aquaria and naturalised individuals. Functional responses differed between species and were mostly higher for spiny-cheek crayfish males. Marbled crayfish, however, were more voracious and reached satiation more slowly. Consumption rates correlated with aggression for marbled crayfish and with an aggressive threat response for spiny-cheek crayfish.
- 4. We conclude that spiny-cheek crayfish can reach higher short-term consumption rates than marbled crayfish, but both species probably do not substantially affect Dreissena mussel populations in the field. For marbled crayfish, high long-term consumption, interspecific aggression, and reproduction rates can promote their establishment and spread. Risk assessments of these invaders should be improved by considering numerical responses, and different prey organisms and predators.

KEYWORDS

biological invasions, foraging, freshwater crayfish, functional response, mechanistic model, predator-prey interactions, trait variation

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1 | INTRODUCTION

As the number of species invasions increases, the understanding of novel communities becomes increasingly pressing (Pacifici et al., 2015; Seebens et al., 2017). These novel communities are often shaped by over-invasions, which take place when an invasive species is replaced by a functionally similar invader (Russell, Sataruddin, & Heard, 2014). When invasives and other novel organisms become part of native communities, they participate in predator-prey and other ecological interactions (Thuiller et al., 2010). Accurately predicting these interactions would enable us to focus management efforts on the most impactful species (Jeschke, Keesing, & Ostfeld, 2013). Information on past interactions are often not available and lack the predictive power to quantify ecological impact and invasiveness of novel species (Kumschick et al., 2014); in addition, trait-based measures of impact are often context dependent and subject to significant variability among species (Leffler, James, Monaco, & Sheley, 2014; Parker et al., 2013). But higher and more efficient resource utilisation is a common characteristic of successful invaders when compared to functionally similar species-it may thus be useful for predicting their impact (Dick et al., 2014, 2017).

1.1 | Functional responses

Trophic interactions and especially predation cause many of the farreaching impacts that invasive species have, including altering community structure and population dynamics (David et al., 2017). The energy and matter in the form of prey or other resources that a novel organism can access are critical for its success in the new environment (Funk & Vitousek, 2007; Mooney & Cleland, 2001). This integral concept of ecology and evolution is ideally described by the functional response, i.e. the relationship of resource consumption at different densities per unit time (Berryman, 1992; Holling, 1959a; Oaten & Murdoch, 1975). Functional responses directly and quantitatively measure per capita interaction strength in nonlinear interactions between a consumer and its resources (Jeschke, Kopp, & Tollrian, 2002; Kalinkat, 2014). They are further linked to measures of energy flow (Marquet, Labra, & Maurer, 2004) and other trait-based characteristics of organisms such as allometric relationships (Kalinkat, Schneider, et al., 2013).

Three major types of functional response are typically discriminated: type I, II, and III (Holling, 1959a); where the type II is most frequently observed in experiments and modelled in theoretical studies (Jeschke et al., 2002; Jeschke, Kopp, & Tollrian, 2004):

$$y(N) = \frac{aN}{1+ahN},$$
(1)

where y is the per capita consumption rate, N is prey density, a is attack rate (also known as rate of successful search, success rate or capture rate), and h is handling time. Equation (1) is the most popular functional response model, Holling's (1959b) disc equation. It has an initial slope determined by *a* and rises towards an asymptote determined by *h*. However, these parameters are simplified. To allow for a biologically meaningful interpretation, they need to be further subdivided: *a* is the product of (1) predator–prey encounter rate, (2) predator detection probability, (3) attack probability, and (4) attack efficiency; *h* is the time a predator needs to successfully attack and ingest prey for certain experimental conditions. Under natural conditions, digestion time can also be very important (Jeschke et al., 2002; Li, Rall, & Kalinkat, 2018).

In a mechanistic framework, the values of these components of both *a* and *h* can be empirically measured (plus digestion time, given the experimental conditions; Jeschke et al. (2002), Li et al. (2018)), and then used to predict a predator's functional response by parameterising a functional response model. If this predicted functional response reasonably matches the independently measured empirical functional response of the predator species, one can assume that the model includes the essential components of the focal system. Such a mechanistic approach is labour-intensive and rarely applied-exceptions include Gergs and Ratte (2009); Holling (1966); Jeschke and Hohberg (2008); Jeschke and Tollrian (2005a); Metz, Sabelis, and Kuchlein (1988). Instead, most studies on functional responses fit Equation (1) or a similar model to empirically measured functional responses. Parameter estimates for a and h derived in this way do not represent what their names suggest: for example, a parameter estimate for h returned by a regression fit of Equation (1) must not be confused with real handling time. Such parameter estimates cannot be interpreted biologically, as they are influenced by digestion, prey switching, learning, or adaptive behaviour in unknown ways (Geritz & Gyllenberg, 2012; Jeschke & Tollrian, 2005b). Conversely, mechanistic models allow for predictions of how the functional response would change if any of the parameters change.

Functional responses are important in classical ecological research, and have been used in invasion biology for about a decade since Bollache, Dick, Farnsworth, and Montgomery (2007) found higher functional responses in invasive *Dikerogammarus villosus* compared to native *Gammarus* species. Since then, higher efficiency in resource use by invaders has been found across taxonomic groups (Alexander, Dick, Weyl, Robinson, & Richardson, 2014; Dick et al., 2013; Xu et al., 2016). However, existing functional response studies focusing on biological invasions have not yet applied a mechanistic approach.

1.2 | Behaviour

Behavioural variation between individual consumers can substantially affect functional responses (Okuyama, 2008). The variation in behavioural types of conspecifics is an important factor in structuring novel communities and changing population dynamics (Bolnick et al., 2011; Chapple, Simmonds, & Wong, 2012; Sih, Cote, Evans, Fogarty, & Pruitt, 2012) and entail important implications for invasion impact (Evangelista, Cucherousset, & Lecerf, 2019). Individual phenotypic variability generally manifests in traits that are important for surviving in a new environment (i.e. functional response traits) and traits that determine the ecological impact of invasive species (i.e. functional effects traits) (Raffard et al., 2017). Rapid increases in population size, as often observed in invasive species, as well as individual growth, require phenotypic traits that facilitate access to large amounts of resources (Biro, Adriaenssens, & Sampson, 2014; Pintor, Sih, & Kerby, 2009). For example, high feeding rates are coupled with high metabolic rates and thus with activity, gut retention time and maximum feeding rates (Rall et al., 2012). Individual activity patterns can predict foraging activity of consumers even when they are not feeding (McGhee, Pintor, & Bell, 2013; Pruitt, Stachowicz, & Sih, 2011). Furthermore, higher aggression and boldness are often correlated to higher foraging rates (Pintor, Sih, & Bauer, 2008). The relationships of behavioural types across a resource gradient (i.e. functional responses and/or their constituent parameters) are largely unexplored (Toscano, Gownaris, Heerhartz, & Monaco, 2016). Some behavioural traits such as explorative behaviour could not be related to functional responses (Schröder, Kalinkat, & Arlinghaus, 2016), but others, such as aggressiveness (Hartley, Shrader, & Chamaillé-Jammes, 2019), activity, and the response to predation threat (Toscano & Griffen, 2014), strongly affected the functional response of individuals.

1.3 | Invasive crayfish

Decapod crustaceans have invaded and subsequently altered freshwater ecosystems worldwide (Twardochleb, Olden, & Larson, 2013). As polyphagous intermediate consumers, they can reduce macrophyte and invertebrate biomass, species diversity, and richness (Mathers et al., 2016; van der Wal et al., 2013). In addition, they threaten native crayfish species by competition, intraguild predation, and transmission of diseases, particularly crayfish plague (*Aphanomyces astaci*; Holdich, Reynolds, Souty-Grosset, & Sibley 2009).

In the wake of crayfish-plague caused extinctions, a rising number of plague-resistant North American crayfish species have established populations and started spreading across Europe (Kouba, Petrusek, & Kozák, 2014). Several of these crayfish have been classified as invasive alien species of European Union concern under Regulation 1143/2014. Two of them are the spiny-cheek crayfish (Faxonius limosus), which has become dominant in central and eastern European water bodies (Kouba et al., 2014), and the marbled crayfish (Procambarus virginalis), which is a relatively recent newcomer. Due to the marbled crayfish's popularity as a pet, aquarium releases have managed to establish a number of populations particularly in Germany (Chucholl, Morawetz, & Groß, 2012). Marbled crayfish are estimated to become a problematic invader and spread beyond their current distribution (Chucholl et al., 2012; Chucholl & Wendler, 2017). They often live in sympatry with spiny-cheek crayfish and attain almost similar sizes (Chucholl & Pfeiffer, 2010; Souty-Grosset, Holdich, Noël, Reynolds, & Haffner, 2006). Marbled crayfish do not naturally occur in the wild and were first described from the German pet trade (Lukhaup, 2001). Its novelty and parthenogenetic mode

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of reproduction make the marbled crayfish especially interesting for biologists (Gutekunst et al., 2018; Martin, Thonagel, & Scholtz, 2016). The ecology and behaviour of this species in the field are virtually unknown, and new information could help estimate the risk of further spread and impact of this new species (Chucholl, 2015; Linzmaier, Goebel, Ruland, & Jeschke, 2018).

Introductions of such non-native species can alter species interactions, for example between predators and prey. Even if similar in size or density compared to resident species, non-native species may have a more flexible diet, be more efficient predators or have higher resource intake rates, thus exerting higher pressure on native communities than resident crayfish (Ercoli, Ruokonen, Hämäläinen, & Jones, 2014; Haddaway et al., 2012; Usio, Suzuki, Konishi, & Nakano, 2006). Strong interspecific aggression and high activity of many invaders limit the accessibility of resources for competitors and puts additional pressure on potential prey organisms (Bubb, Thom, & Lucas, 2006; Pintor et al., 2008). The mechanisms behind the changes brought by new and novel crayfish can only be understood when individual interactions with other organisms are considered.

1.4 | Aims of this study

We implemented the trophic interaction framework developed by Penk et al. (2017) and used comparative functional responses to predict changes in an invaded community by changes in interaction strength. We compared the focal novel organism (marbled crayfish) with the most similar species that is already present in the community of our reference lake (spiny-cheek crayfish in Lake Müggelsee, Berlin, Germany). We then identified an important potential prey in the target community that has high biomass and represents a keystone organism. Mobile prey (e.g. Ephemeroptera species) are often not as much affected as non-mobile prey (e.g. mussels) (Hanson, Chambers, & Prepas, 1990; Mathers et al., 2016). Also, invasion success is likely when highly abundant prey can be utilised (Tilman, 2004). Thus, we chose Dreissena mussels as prey; they occur at extremely high biomasses and are readily consumed by crayfish (zu Ermgassen & Aldridge, 2011; Perry, Lodge, & Lamberti, 2000). Dreissena mussels are ecosystem engineers and have massively reshaped ecosystems in Europe and North America by filtration and epibiosis (Ricciardi, 2003); high predation rates on these mussels may thus substantially affect aquatic ecosystems (Karatayev, Burlakova, & Padilla, 2002). Marbled crayfish were expected to have a higher functional response due to their recent invasion success.

Further, we aimed at a mechanistic understanding of this process by identifying trophic traits that promote invasions and investigate the effect of individual behavioural types on these traits and the functional responses, bringing together research on animal personality and food-resource use (Toscano et al., 2016). In an additional set of experiments, we independently measured all stages of the predation cycle (functional response parameters) for individual crayfish. We then quantitatively compared the functional response NILEY- Freshwater Biology

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to our model predictions. We hypothesised that feeding parameters derived in separate experiments would describe the functional response of both species. Finally, previously assessed behavioural types of the tested individuals were compared to functional responses and functional response parameters. We expected active, bold, and aggressive individuals to have higher functional responses and higher functional response parameters.

2 | METHODS

2.1 | Study sites

Individuals from three populations of crayfish were collected for the experiments. First, we caught spiny-cheek crayfish in Lake Müggelsee close to our institute (52°26′6″N, 13°38′6″E), Germany, with baited (dogfood) crayfish traps (type PIRAT, 610 × 315 × 250 mm, mesh width 40 × 10 mm, Rapurosvo) between April 2015 and June 2016. The traps were set over night and checked on the next day. Second, marbled crayfish were taken from aquarium stocks kept by Peer Martin (Comparative Zoology, Humboldt University, Berlin, Germany). And third, we caught naturalised marbled crayfish by hand (and to a minor degree, by traps) from stocks that live in sympatry with spiny-cheek crayfish and *Dreissena* mussels in the littoral zone from lakes (1) Moosweiher (48°01′51″N, 7°48′17″E) in Baden-Württemberg, Germany, and (2) Krumme Lanke (52°27′0″N, 13°13′52″E) in Berlin, Germany.

We sexed and measured all crayfish manually with a sliding calliper to the nearest millimetre. Length was measured as carapace length (CL) from the tip of the rostrum to the posterior edge of the carapace.

2.2 | Maintenance of test animals

Crayfish were maintained in a climate chamber (17°C, 14 hr light: 10 hr dark). All crayfish were kept in the laboratory for at least 1 month before being used in experiments. All individuals used for measurements on behaviour and feeding were single-housed in tanks $(300 \times 200 \times 200 \text{ mm})$ that were filtered by air-driven sponge filters. Only naturalised marbled crayfish from the Lake Moosweiher population were marked for differentiation among individuals, and kept in filtered single-species community tanks ($800 \times 400 \times 200$ mm). We marked them with a point-code on top of their carapace using a white outdoor marker (Edding 8055; see Abrahamsson, 1965). We waited about a week before remarking and measuring crayfish following moulting events. One PVC pipe (150 mm, Ø 50 mm) was provided as shelter, and 30 mm of fine gravel was put in each tank as a substrate. Additional shelters (>2 per crayfish) were provided in the communal tanks to reduce agonistic interactions. Water was exchanged with fresh tap (c. 75%) water once a week. Half a ring of commercial crayfish food (Crabs natural, sera) was fed to each crayfish daily.

The protocol and procedures employed were ethically reviewed and approved by the Landesamt für Gesundheit und Soziales (LAGeSo), Berlin, Germany. All experiments were performed in accordance with Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes.

2.3 | Setup and standard procedure

Experiments were conducted between June 2015 and April 2017. All trials took place in the climate chamber to reduce handling and guarantee minimal disturbance from outside. Each setup was sheathed by opaque, black plastic tarpaulin to further minimise disturbances. Handling time experiments, parameter measurements and satiation measurements were filmed by two network cameras (Dinion HP 1080p, Bosch; one vertically above the tank and another one at the side of the tank). Videos were recorded under infrared illumination (except handling time) from infrared headlights under total darkness. VLC-player (version 2.2.1.0) was used to record and save video data.

Before crayfish were used in any experiments, we checked them for loss of appendages, obvious diseases, eggs, upcoming moulting events and the current reproductive form (form I/II in spiny-cheek crayfish males). We tested randomly chosen male and female spinycheek crayfish (using a pair of 10-sided dice), as consumption is generally assumed to be independent of sex (Usio & Townsend, 2002). Intact intermoult individuals (26–50 mm CL) were used in experiments only for one trial per day. Crayfish were excluded from experiments up to at least 1 week when either moults occurred or after the release of brood by egg-bearing female because crayfish reduce or cease feeding completely during ecdysis (Aiken & Waddy, 1992).

Experimental tanks were filled with 20 mm of fine white sand and 150 mm of tap water of 15°C temperature. Crayfish were released into the tank and allowed to acclimatise for 30 min prior to the start of experiment. Tanks were completely drained after each trial, and before setting up another experiment to avoid a potential bias by remaining pheromones in the water (Breithaupt, 2011).

Dreissena mussels were collected at Lake Müggelsee by hand-picking them off hard structures on a weekly basis. We refer to them as Dreissena mussels since meaningful differentiation between the two species present in Lake Müggelsee, the zebra mussel (Dreissena polymorpha) and the quagga mussel (D. rostriformis), can only be done by genetic means (Beggel, Cerwenka, Brandner, & Geist, 2015). After collection, mussels were kept separately in an aerated tank until required.

2.4 | Size selection

To determine the optimal prey size for our experiments, we performed size-selection trials with spiny-cheek crayfish males (n = 7, CL = 34.2, SD = 2.7), spiny-cheek crayfish females (n = 6, CL = 37.2, SD = 2.8), and marbled crayfish from aquaria (n = 12, CL = 33.3, SD = 3.3). We offered crayfish four different size classes of Dreissena mussels: 2–6 mm (n = 10), 7–11 mm (n = 10), 12–16 mm (n = 10), and 17–21 mm (n = 10). A single crayfish was placed into a tank measuring 400 × 400 × 200 mm with the mussels and a PVC pipe for shelter. After 24 hr we counted the remaining mussels of each size class that were still alive.

2.5 | Functional response model

As basic functional response model, we used the Royama-Rogers random predator equation (Rogers, 1972; Royama, 1971) which is an extension of Holling's (1959b) disc equation (Equation 1) and accounts for prey depletion. For this model, we used the notation derived by Rosenbaum and Rall (2018):

$$y(N_{0}) = \frac{N_{0} - W(ahN_{0} * \exp(a(hN_{0} - T)))}{ah}.$$
 (2)

The model includes the number of mussels initially offered to the experimental predator (N_0), the LambertW function (W), attack rate (*a*), handling time (*h*) and total experimental time (*T*).

We derived the values for these parameters by carrying out experiments for three treatment groups: spiny-cheek crayfish males (n = 12), spiny-cheek crayfish females (n = 7), and marbled crayfish from aquaria (n = 15). During the long course of experiments three marbled crayfish, three spiny-cheek crayfish females, and two male spiny-cheek crayfish got sick or died during moults and thus had to be excluded from the study. The experiments for deriving parameter values (see Sections 2.6 and 2.7) were separated from those that we carried out to empirically measure functional responses (see Section 2.9).

We decided to run short-term experiments of T = 1 hr, as the crayfish consumed many mussels per unit time within the restrictions of our tanks (Jeschke et al., 2002). For such a short time period, satiation effects should be minimal. We therefore decided not to include such effects in the model (cf. Jeschke & Hohberg, 2008; Jeschke et al., 2002; Jeschke & Tollrian, 2005a). We conducted separate experiments to look into the effects of satiation (see below). To parameterise the model and mechanistically predict crayfish consumption rates *y*, it was necessary to express *a* and *h* in more detail, so that they can be directly experimentally measured.

2.6 | Attack rates

We followed Jeschke et al. (2002) to calculate attack rate (a):

$$a = \beta \times \gamma \times \delta \times \varepsilon. \tag{3}$$

Accordingly, we experimentally quantified each of the parameters in Equation (3) for individual spiny-cheek crayfish males Freshwater Biology -WILEY

(n = 10, CL = 35.4, SD = 2.3), spiny-cheek crayfish females (n = 4, CL = 35.4, SD = 2.3)CL = 33.2, SD = 3.8), and marbled crayfish from aquaria (n = 12, CL = 33.0, SD = 3.9). We calculated encounter rate β , probability of detection γ combined with probability of attack δ , and attack efficiency ε for (1) each trial, (2) as mean values for each individual crayfish, and (3) as mean values for each species. Attack efficiency in each trial was calculated as the number of successful attacks (cracking and feeding of the mussel) divided by the total number of attacks. Probability of detection and probability of attack cannot be visually distinguished here. The product of these two was calculated as the number of attacks divided by the number of encounters with the mussel. Generally, we observed that close proximity with the appendages of the crayfish seemed to be necessary for an attack under laboratory conditions (i.e. total darkness). An encounter was recorded when the mussel and the encounter field overlapped. The ellipsoid encounter field of a cravfish was approximated by the length between the end of the antennae and the end of the carapace, and the width of the first pereiopods with the base of the rostrum in the centre (Giguère, Delâge, Dill, & Gerritsen, 1982). To measure encounter rate β , we counted the number of encounters and divided them by the mean number of mussels during the trial. This number was then multiplied by 60 (min) and divided by the time spent searching during the trial in minutes to yield encounter rate β per hour for that particular trial. The time spent searching was trial time minus time spent handling mussels (Section 2.7).

The setup described in size selection experiments was used here again, and 20 mussels, each between 3 and 7 mm in size (shell length), and 4 and 40 mg in weight, were randomly distributed on the sandy bottom of the tank. The experiments were conducted in the dark when crayfish are most active and illuminated by infrared headlights (Holdich & Black, 2007; Luna, Hurtado-Zavala, Reischig, & Heinrich, 2009). We visually analysed 17 hr of videos and measured parameters for 30 min after the first mussel was consumed. If the crayfish consumed fewer than five mussels during this time, the experiment was repeated on another day.

2.7 | Handling times

We measured the components of handling time h as outlined in (Jeschke et al., 2002):

$$h = \frac{t_{\text{att}}}{\varepsilon} + t_{\text{eat}},\tag{4}$$

where t_{att} is attacking time per prey item, t_{eat} is eating time per prey item and e is attack efficiency. The latter was measured as outlined in the previous section and is included in Equation (4) because handling time includes time wasted through unsuccessful attacks (Jeschke et al., 2002).

We measured both mean t_{att} and t_{eat} (n = 3–12) of the aforementioned individuals of spiny-cheek crayfish males (CL = 33.4, SD = 4.0), WII FY- Freshwater Biology

spiny-cheek crayfish females (CL = 33.0, *SD* = 3.7), and marbled crayfish from aquaria (CL = 35.8, *SD* = 2.6). Crayfish were put in a tank with the dimensions $300 \times 200 \times 200$ mm. After acclimatisation, a single crayfish was provided with 20 *Dreissena* mussels (same size range as in *attack rates*). Feeding was recorded under low light conditions for better resolution. We stopped recording after 20 min or until five mussels were consumed. The 11 hr and 20 min of recordings were later visually analysed for the handling parameters according to the following definitions: attacking time per mussel, the time spent during a predation attempt, was defined as the time from the moment of first contact with the mussel to the moment it is cracked; eating time per mussel started when the crayfish feeds upon the mussel's flesh to the moment the mussel is abandoned (zu Ermgassen & Aldridge, 2011).

2.8 | Satiation

We estimated satiation per crayfish by recording a subset of individual spiny-cheek crayfish males (n = 8, CL = 38.3, SD = 2.4), spiny-cheek crayfish females (n = 2, CL = 37.8, SD = 2.7), and marbled crayfish from aquaria (n = 6, CL = 38.3, SD = 2.5) feeding on 300 *Dreissena* mussels for 3 hr in the dark. We visually analysed 90 hr of video recordings and noted the time at which the crayfish consumed a mussel in each trial. We presumed that crayfish become satiated with time, and the resulting cumulative consumption in a hungry crayfish will rise sharply with time at the beginning and less so when they had filled their guts (Elliott & Persson, 1978; Jeschke & Hohberg, 2008). After the experiment, we relocated the crayfish in its holding tank and sieved the sand with dip nets to remove all remaining mussels, faeces and debris of feeding activity.

To estimate the point of transition between hunger and satiation, we performed breakpoint analysis for the count of mussels and the time between two consumed mussels (command breakpoints from the package *strucchange* [Version 1.5-1; Zeileis, 2006]). The breakpoint is the point after which the time period between mussel consumptions increases and which we equated with a full gut. The satiation per mussel *s* is the reciprocal value of the number of mussels in a full gut (Jeschke et al., 2002). For example, crayfish S9 had a full gut after having consumed 85 mussels; its satiation per mussel *s* was thus 0.012 (Table S1). In the next step, we estimated maximum long-term consumption y_{max} , i.e. the maximum number of mussels consumed at an excess of prey including satiation, by fitting logarithmic models to the consumption rate over 15-min time intervals. Finally, we calculated gut retention time t_g as $1/(y_{max} \times s)$ (cf. Jeschke et al., 2002).

2.9 | Functional response experiments

Following the parameterisation of the functional response model for each crayfish species, we empirically measured the functional responses in order to compare model predictions with observed consumption rates. These experiments were run in the same tanks under the same preconditions as the parameter experiments on *a* and *h*. We used the same individual spiny-cheek crayfish males (mean CL = 36.9, *SD* = 1.9 mm), spiny-cheek crayfish females (mean CL = 35.1, *SD* = 2.8 mm), and marbled crayfish from aquaria (mean CL = 34.1, *SD* = 3.4 mm) tested for functional response parameters because these were later related to personality traits (Section 2.10). In addition, we used naturalised marbled crayfish (*n* = 7, CL = 39.5, *SD* = 6.6 mm), which were significantly larger than aquarium individuals (two-sided *t* test for unequal variances: *df* = 125, *t* = -7.158, *p* < 0.001), to be able to also compare their functional responses to those of the groups of crayfish.

During the experiments, the crayfish were supplied with 20, 30, 40, 50, 60, 80, and 100 *Dreissena* mussels of the same size as for previous experiments. Three to five replicates at each density for each individual and within each treatment were measured in n = 969 feeding trials. Crayfish were left feeding on the mussels for 1 hr in darkness. We then removed the crayfish and sieved the sand for the feeding remains as described for the satiation experiment. The remaining mussels that were still alive or damaged but not consumed were then counted. If crayfish refused to feed and moulted (n = 140) or had a new clutch (n = 41) following the experiment within 1 week, values were excluded from the dataset.

We calculated mean numbers of consumed mussels for each density for each individual. We then calculated species means for spiny-cheek crayfish, marbled crayfish from aquarium, and naturalised crayfish for each density and compared them to each other and the associated model. To account for size differences caused by moulting events between the experiments, we also calculated size-corrected models using the mean sizes measured during functional response trials (Figure S1).

2.10 | Behavioural assay

In a previous study (Linzmaier et al., 2018), we performed personality experiments with the same individuals that have been used here in functional response experiments. Individuals were tested for differences in activity, aggressiveness, and boldness: aggression during interspecific confrontations was scored with the system developed by Atema and Voigt (1995); activity was assessed as the proportion of time spent inside and outside a shelter during 6 hr of observation; and boldness was measured as the response of a crayfish to an approaching human hand. Further details on the behavioural assay can be found in Linzmaier et al. (2018). The individuals of both species were divided into two groups each by their mean activity (low and high activity), aggression score (low and high aggression), and aggressive (positive score) or fearful threat response (negative score). We pooled male and female spinycheek crayfish here due to low sample size of the subgroups. We calculated means for each prey density from all individuals of the group. We then assessed if functional responses differed between these groups.

2.11 | Statistics

Means of a, h, s, and y_{max} were statistically compared by two-sided t tests (Dick et al., 2013). The relationship between predicted and measured consumption (i.e. the mechanistic model) was determined by Pearson's product-moment correlation. Functional response type of the measured functional responses was determined following Juliano (2001) by visual inspection of raw plotted data and the frair test function, provided by the frair R-package (Version 0.5.100; Pritchard, Paterson, Bovy, & Barrios-O'Neill, 2017) to test whether a type II or type III curve better fits the data. We further evaluated the measured functional responses by fitting regression models to the data of each group (based on Royama-Rogers random predator equation as above), and calculating 95% confidence intervals by bootstrapping (n = 999) (Pritchard et al., 2017). As starting values for each model fit, we used the measured parameter (a and h from 2.6 and 2.7) from each group for free model parameters and T = 1 hr. We then looked at overlaps of the confidence intervals between marbled crayfish, spiny-cheek crayfish females, and spiny-cheek crayfish males. We also compared aquarium with naturalised marbled crayfish in this way. Additionally, we created a correlation matrix for all individuals mentioned above, including female spiny-cheek crayfish (package Hmisc; Harrell and Dupont (2018); method = Pearson).

3 | RESULTS

3.1 | Models and observed consumption

The observed functional response was consistently higher for spiny-cheek crayfish males and females compared to marbled crayfish (Figure 1). This was also the case when correcting for size differences among crayfish (Figure S1). Marbled crayfish had a significantly lower functional response than male spiny-cheek crayfish but not spiny-cheek crayfish females; spiny-cheek crayfish females had lower functional response than males (Figure S2). Naturalised marbled crayfish had a slightly higher, although not significantly different functional response compared to aquarium marbled crayfish (Figure S2). The curve progression we observed can best be described by a type II functional response (spiny-cheek males: z = -14.80, p < 0.001; spiny-cheek females: z = -8.10, p < 0.001; marbled crayfish: z = -7.93, p < 0.001). The predicted model fit was best for male spiny-cheek crayfish (r = 0.87, t = 14.26, p < 0.001), but also good for both female spiny-cheek crayfish (r = 0.78, t = 6.32, p < 0.001) and marbled crayfish (r = 0.80, t = 11.80, p < 0.001). The mechanistic models adequately predicted the functional responses but slightly overestimated it overall.

3.2 | Parameters

The handling time (*h*) of male spiny-cheek crayfish was significantly shorter than that of marbled crayfish (Table 1; df = 20, t = 2.76, p =

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0.012). Female and male spiny-cheek crayfish (df = 12, t = 2.05, p = 0.063) as well as female spiny-cheek crayfish and marbled crayfish (df = 14, t = 0.65, p = 0.526) did not significantly differ in *h*. Attack rate (*a*) did not significantly differ between species or sexes (df = 20, t = 1.30, p = 0.207; df = 12, t = 0.77, p = 0.455; df = 14, t = 0.05, p = 0.961). This comparison also includes satiation parameters: Long-term maximum feeding rates were higher for marbled crayfish (df = 12, t = 2.96, p = 0.012). Marbled crayfish did not have a higher gut capacity (df = 12, t = 2.04, p = 0.064) and therefore gut retention time than spiny-cheek crayfish males (Table 2).

3.3 | Size selection

Both crayfish species preferred smaller mussels up to 11 mm over larger ones when given the choice between different size classes (Figure S3). Marbled crayfish generally consumed fewer mussels than spiny-cheek crayfish.

3.4 | Behaviour and functional response

We found that highly versus less active individuals of both marbled crayfish (Figure 2a; a: df = 9, t = 1.71, p = 0.122; h: df = 9, t = 0.87, p = 0.409) and spiny-cheek crayfish (Figure 2b; a: df = 12, t = 0.39, p = 0.705; h: df = 12, t = 0.26, p = 0.800) did not significantly differ in numbers of consumed mussels. Marbled crayfish with higher aggression scores had higher h (df = 11, t = 2.21, p = 0.049) and thus higher functional responses at high prey densities compared to individuals with low aggression scores (Figure 2c), whereas a did not significantly differ (df = 11, t = 1.63, p = 0.131). The predicted functional response models for the more aggressive individuals confirmed the measured values, slightly overestimating the consumption except for the highest prey numbers. No difference between the groups was found among spiny-cheek crayfish (Figure 2d; a: df = 12, t = 0.27, p = 0.793; h: df = 12, t = 0.17, p = 0.17, 0.864). Bolder spiny-cheek crayfish with an aggressive threat response exhibited a higher functional response and had a significantly lower h (Figure 2f; df = 12, t = 3.09, p = 0.009), whereas a did not significantly differ (a: df = 12, t = 0.13, p = 0.898). The aggressive individuals were mostly male (one female) and the fearful individuals mostly female (one male; see Linzmaier et al., 2018). The predicted functional response models confirmed these patterns for spiny-cheek crayfish (Figure 2f) and to a minor degree for marbled crayfish, while their measured data do not suggest this difference (Figure 2e).

3.5 | Bivariate correlations

The multivariate correlations on the species level revealed similar patterns of correlations among variables in each species with some exceptions (Figure 3a,b). In individuals of marbled crayfish,



	Marbled crayfish (n = 12)	Spiny-cheek crayfish (♀, n = 4)	Spiny-cheek crayfish (ਾ, n = 10)
Encounter rate β (h ⁻¹) ^a	6.84, SD = 2.83	6.07, SD = 3.20	7.62, SD = 3.46
Detection probability $\gamma \times \text{attack probability}$ attack δ^{a}	0.48, SD = 0.15	0.58, SD = 0.19	0.54, <i>SD</i> = 0.18
Attack efficiency ε^{a}	0.93, <i>SD</i> = 0.07	0.87, SD = 0.14	0.93, <i>SD</i> = 0.08
Attacking time $t_{\rm att}$ (s) ^b	21, SD = 9	21, SD = 6	17, SD = 7
Eating time $t_{\rm eat}$ (s) ^b	56, SD = 17	45, SD = 8	36, SD = 7
Handling time <i>h</i> (s) ^c	79, SD = 26	70, <i>SD</i> = 14	54, SD = 13
Total attack rate a (h ⁻¹) ^c	2.81, SD = 1.09	2.84, SD = 1.38	3.61, <i>SD</i> = 1.78

FIGURE 1 Observed functional responses (means \pm *SE*) for marbled crayfish, spiny-cheek crayfish females and spiny-cheek crayfish males and the functional response predicted from independently derived parameters. The number of mussels refers to one experimental area (0.16 m²) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Means and SD of measuredand calculated predation parameters formarbled crayfish and spiny-cheek crayfishfrom foraging observations on Dreissenamussels

^aParameter experiment.

^bHandling time experiment.

^cCalculated from parameters above (see Equations 3 and 4).

aggression was negatively correlated with *a*. Activity was positively correlated with aggression and ε for marbled crayfish (see Linzmaier et al., 2018) and negatively correlated with y_{max} for spiny-cheek crayfish. More aggressive threat response scores were negatively correlated with *h* and t_{att} for spiny-cheek crayfish and positively with ε for marbled crayfish. The parameter *h* was naturally positively correlated with its constituent parameters, and *a* was positively correlated with β for spiny-cheek crayfish (see Equations 3 and 4). The γ and t_{att} were positively correlated for marbled crayfish.

4 | DISCUSSION

We investigated the trophic interactions of two co-occurring invasive crayfish species and mussel prey with the framework developed by Penk et al. (2017). We looked at foraging and feeding parameters, the functional responses and behavioural types of single individual crayfish. Hereby, we gained a detailed mechanistic understanding of the studied predator-prey interaction. The observed interaction strength provides an estimate of relative impact potential of two invasive crayfish on an ecologically important invasive mussel. Further, we could adequately predict the relative interaction strength for two invasive crayfish on ubiquitous *Dreissena* mussel prey with our models. The detailed measurements showed that males of the widely established spinycheek crayfish outperformed naïve, aquarium as wells as sympatric, naturalised marbled crayfish on most aspects of feeding on *Dreissena* mussels. Feeding modalities and behavioural differences among individuals might explain some aspects of effectiveness in prey consumption. TABLE 2Means and SD of satiationparameters for marbled crayfish andspiny-cheek crayfish

Parameter	Marbled crayfish (n = 6)	Spiny-cheek crayfish (♀, n = 2)	Spiny-cheek crayfish (♂, n = 8)
Number of prey items for satiation (g) ^a	96, SD = 8	95, SD = 2	80, <i>SD</i> = 17
Maximum long-term consump- tion (y _{max} [d]) ^a	779, SD = 128	612, SD = 51	558, SD = 145
Gut retention time $(t_g [h])^b$	3.10, <i>SD</i> = 0.59	3.77, SD = 0.35	3.62, SD = 0.56

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^aSatiation experiment.

^bCalculated from satiation parameters above (see main text).

FIGURE 2 Predicted and observed functional responses (means \pm *SE*) for marbled crayfish (left column) and spinycheek crayfish (right column) of different behavioural types (a, b = activity; c, d = aggression; e, f = threat response). The number of mussels refers to one experimental area (0.16 m²) [Colour figure can be viewed at wileyonlinelibrary.com]



4.1 | Functional responses

The mechanistic models performed well in predicting the difference observed in the functional response between both species. Both species showed type II responses. This type of response has also been found in red swamp crayfish (*Procambarus clarkii*) feeding on *D. polymorpha* (Gonçalves, Gherardi, & Rebelo, 2017). The functional response curve can be influenced by many factors including habitat complexity (Kalinkat, Brose, & Rall, 2013). Structurally complex habitats provide shelter for prey, especially at low densities. Oyster shell habitats, for example, increased *a* differently for small and large mud crabs at low prey densities



FIGURE 3 Correlation matrices of behavioural variables (aggression, activity and threat response) and feeding variables (attacking time per prey item $[t_{att}]$, eating time per prey item $[t_{eat}]$, attack efficiency [ε], encounter rate [β], probability of detection [γ], handling time (h), attack rate [a], maximum long-term consumption [y_{max}] and satiation per mussel [s]) in (a) a set of individual marbled crayfish and in (b) a set of individual spiny-cheek crayfish. Each cell contains the correlation coefficient, and significant ($\alpha = 0.05$) correlations are represented by coloured squares. Red colours indicate negative correlations and blue colours positive correlations [Colour figure can be viewed at wileyonlinelibrary.com]

and resulted in type III functional responses whereas less complex habitats resulted in type II functional responses (Toscano & Griffen, 2013, 2014). *Dreissena* mussels usually are easily accessible, settling on every hard surface available and live even on flat, soft, and open sediments in large densities making a type II response also in the field very likely (Dermott & Munawar, 1993). Some factors could still alter the predation process. *Dreissena* mussels seek refuge and form firm aggregations in response to predation (Kobak & Kakareko, 2009; Naddafi & Rudstam, 2013). Prey aggregations should lead to a decrease in β . This had been shown in signal crayfish (*Pacifastacus leniusculus*) feeding on *Dreissena* mussels which spent significantly more time foraging for single *Dreissena* mussels compared to druses of mussels (zu Ermgassen & Aldridge, 2011). However, feeding rate was not different between single mussels and druses. We thus believe that our measurements realistically captured the foraging process on *Dreissena* mussels.

In contrast to our predictions, marbled crayfish had a lower functional response than male spiny-cheek crayfish. These might have been affected by egg production and care periods of marbled crayfish. Due to their parthenogenetic reproduction, our isolated marbled crayfish were still able to reproduce several times during the course of the experiments. This was not the case for spiny-cheek crayfish, that are sexually reproducing. Generally, marbled crayfish reduced or ceased feeding during reproduction, but we could also observe feeding individuals during reproduction. We do not know the exact times of reduced feeding, but the 1 week after release of the young that we set as limits before continuing measurements might have been too arbitrary.

4.2 | Parameters and satiation

Feeding rates (this study) and boldness (Linzmaier et al., 2018) differed for male and female spiny-cheek crayfish. Usio and Townsend (2002) found that male *Paranephrops zealandicus* had higher feeding rates than females when feeding on leaf litter. Food conversion is usually the same for both sexes (Rodgers, Saoud, & Rouse, 2006). In crayfish aquaculture, however, male crayfish of several species grow faster than females, especially in monosex cultures (Lawrence, Cheng, Morrissy, & Williams, 2000). Hence, higher feeding rates for males could be assumed. However, in several cambarid crayfish feeding on *Dreissena* mussels, no differences or even higher feeding rates of females have been documented (Corkum & Cronin, 2004; Maclsaac, 1994; Perry, Lodge, & Lamberti, 1997). We think that behavioural or developmental differences could explain the differences we found between sexes.

Like all Cambaridae, spiny-cheek crayfish males and even females alternate between a sexually active form I and a non-reproductive form II (Hobbs, 1974; Wetzel, 2002). Higher aggression and sexual activity of form I males have been documented (e.g. Dunham & Guiasu, 1997). Thus, form I males could have a higher energetic demand than form II males, and might consequently have a higher consumption rate. Our measurements were taken over two or three moultings and according to form alterations. We recorded form alterations for male crayfish and found higher functional responses in form I compared to form II males, which in turn consumed more than females (Figure S4). Hence, we think that feeding differences are highly dependent on reproductive stage and individual behavioural types.

Generally, spiny-cheek crayfish seemed to overcome marbled crayfish in most aspect of feeding. However, we found higher physiological capacity for marbled crayfish: they had a significantly higher maximum consumption rate y_{max} . Satiation models capture

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an important element of predation connecting ecological processes and physiology (Jeschke et al., 2002). How can we explain the apparently higher physiological capacity of marbled crayfish? In Linzmaier et al. (2018), we did not observe significant differences in activity between marbled and spiny-cheek crayfish, but metabolic demand of marbled crayfish could still be higher for marbled crayfish due to reproduction (see above). Also, marbled crayfish might have a more efficient conversion of resources to tissue or offspring as it has been found in other invaders (Byers, 2000). This can, for example, come from increased enzyme activity. Johnston and Freeman (2005) found differences in enzyme activity of six species of shore crab, related to their preferential diet. Marbled crayfish seem to have an efficient metabolism that enables them to use feeding periods between rapidly alternating periods of moults and egg-bearing.

4.3 | Impact

The observed per capita effect in the predatory impact of marbled crayfish on Dreissena mussels classifies them as a marginally impactful species according to the literature of comparative functional responses (Dick et al., 2014, 2013). Such relationships have often been related to impact of crayfish on their native counterparts. For example, the functional response of invasive signal crayfish on amphipod prey has been higher compared to white-clawed crayfish (Austropotamobius pallipes) (Haddaway et al., 2012; Taylor & Dunn, 2018). In our case, however, we studied an established, invasive species and a recently arrived novel species (i.e. a co-invasion or even an over-invasion scenario) (Russell et al., 2014). This comparison reflects the ecological reality in many Central European water bodies and has much broader implications than comparisons against the ever rarer native noble crayfish (Astacus astacus) (Kouba et al., 2014). Also, comparisons at an early stage of the invasion or even before transport are more useful for risk assessment than a posteriori studies on higher impact of invaders (Leung et al., 2002).

The high maximum long-term consumption in marbled crayfish could have an effect on Dreissena mussel populations in the field, which impose an impactful invader by themselves. Some predators (native or invasive) potentially provide biotic resistance to invasive prey (Twardochleb, Novak, & Moore, 2012). Blue crab (Callinectes sapidus), for example, significantly reduced zebra mussel populations in parts of the Hudson river (Carlsson, Bustamante, Strayer, & Pace, 2011). Also, field studies on rusty crayfish (Faxonius rusticus) suggest that streams with moderate to high densities of crayfish will limit spread and densities of zebra mussels (Perry et al., 1997, 2000). While crabs also feed on larger, adult mussels, many crayfish species have been shown to prefer smaller prey (zu Ermgassen & Aldridge, 2011; MacIsaac, 1994). We could confirm that also spiny-cheek and marbled crayfish mostly fed on mussels that were smaller than 12 mm. This size class offers the greatest profitability for crayfish (Gonçalves et al., 2017). Thus, Dreissena mussels can reach a size refuge, and mostly small individuals will be impacted by crayfish predation. Additionally, Dreissena mussels adapt their behaviour and

morphology to predation by reducing feeding rate and increasing shell thickness at the cost of lower growth rates (Naddafi & Rudstam, 2013, 2014).

Even in omnivores such as crayfish, we can have different impacts on the food web by new invaders (Larson, Twardochleb, & Olden, 2017). In the field, the interaction strength between marbled and spiny-cheek crayfish plus their prey might be different due to the density of each species. New impact metrics for emerging invasives such as the relative impact potential consider species-specific predation rates and numerical responses in concert with functional responses (Dick et al., 2017). Marbled crayfish might have lower functional responses but have a faster reproduction and may thus reach higher abundances.

Besides the insight that we gained on the predator-prey relationship among crayfish and *Dreissena* mussels, the question remains of whether the observed differences are conserved across prey types. Omnivore decapod crayfish feed on several types of prey, an abundant alternative prey, such as the invasive amphipod *D. villosus*, might shift the pattern of the overall response (Gergs & Rothhaupt, 2008; Smout et al., 2010). Also, macrophytes or detritus might be differently affected, as they are consumed and provide refuge at the same time (Médoc, Thuillier, & Spataro, 2018). Ideally, future comparisons include multiple prey items as well as (average) abundance data of prey organisms in water bodies threatened by invasion.

Finally, invasive species sometimes do not even have to be more aggressive, be better in acquiring resources or exploit a new niche but have less intraspecific competition also called *friendly release* to be successful (Warren et al., 2019). The almost genetically identical, all-female populations of marbled crayfish, for example, have the advantage that they do not have to compete for partners and that genetic similarity reduces aggression (Carazo, Tan, Allen, Wigby, & Pizzari, 2014; Vogt, 2008).

4.4 | Behaviour

Intraspecific variability in prey consumption plays an important role in community dynamics (Des Roches et al., 2018; Raffard et al., 2017). For example, Evangelista et al. (2019) found that the effect of intraspecific variability among invasive red swamp crayfish on prey community responses, especially on leaf litter and snails, was higher than the effect of species presence (invasion) alone. Our expectations on the effects of behavioural types on functional responses and their parameters were partially met. Bolder spiny-cheek crayfish, and to a lesser degree also aggressive marbled crayfish, showed consistently higher functional responses which was confirmed by the model predictions of these individuals. Bolder spiny-cheek crayfish were mostly male and females that fled more often (Linzmaier et al., 2018). In general, females have smaller claws and are less able to defend themselves (Stein & Magnuson, 1976). However, we also had a very fearful male and a very bold female, and believe that individual boldness can affect sex-based models. Marbled crayfish generally did not show a truly WILEY Freshwater Biology

aggressive threat response. They were either ducking away from the approaching hand or fleeing (Linzmaier et al., 2018). Thus, the bolder individuals were classified by *not fleeing*, whereas spinycheek crayfish showed a meral spread and an aggressive approach.

Elevated activity levels seemed not to affect crayfish feeding patterns, but aggression slightly elevated feeding rates by lower hin marbled crayfish. Behavioural correlations or syndromes (Bell & Sih, 2007), like aggression syndromes, can couple activity and aggressive behaviours, which are also important for population establishment of invasive species, with feeding rates (Pintor et al., 2009). In our case, such a syndrome has been found for marbled crayfish but not for spiny-cheek crayfish (Linzmaier et al., 2018). Higher aggression, however, does not necessarily mean higher food uptake. Invasive yabby (Cherax destructor), for example, won less agonistic encounters with the native Fitzroy falls crayfish (Euastacus dharawalus), but were more efficient in feeding on a provided food source (Lopez, Hendry, Wong, & Davis, 2019). The same has been shown for invasive green crabs (Carcinus maenas) and their native comparators, the blue crabs (MacDonald, Roudez, Glover, & Weis, 2007). Therefore, the relationship of aggression and higher feeding rates could indeed be negative. High aggression and lower functional responses of marbled crayfish might thus be retained in the face of direct competition.

We showed that some behavioural types might per se be related to individual differences in feeding parameters. In most studies, values for feeding parameters (a and h) are not mechanistically measured but instead calculated from fitting functional response models (Hartley et al., 2019; Schröder et al., 2016; Toscano & Griffen, 2014). As outlined above, these values must not be confused with real success rate and handling time. Thus, their relationship with measured behaviours cannot be mechanistically interpreted. Here we measured real individual-level functional responses and mechanistic parameters separately and linked them to important behavioural traits. Schröder et al. (2016) could not find such a relationship of parameters derived by phenomenological models in Heterandria formosa killifish feeding on Artemia salina nauplii and suggested that a connection of behavioural traits with feeding might be required. In our study, these patterns of elevated functional responses in more aggressive or bolder individuals could not be seen as a general pattern within both species but only in some instances. However, the predicted models from parameter measurements usually reflected the hypothesised patterns. Maybe these differences get more pronounced when feeding takes place under field conditions. Competition for food will influence interspecific aggression, and interference by predators affects activity and boldness (Pintor et al., 2008). Assessments like ours should therefore be extended by including higher-order predators or direct competition (see Penk et al., 2017).

Looking at the relationship of certain parameters and behavioural traits, we found that bolder and aggressive individuals (aggression against predators and competitors) had shorter h, favouring food uptake at high prey densities. Voracious feeding (high a and short h) was expected for both behavioural types, but this correlation could only be confirmed for the boldness scores. Such

relationships have been found in, for example, signal crayfish were aggression, voracity and boldness were positively correlated with prey consumption rates (Pintor et al., 2008). Bolder individuals are usually higher-ranking in social hierarchies. These hierarchies can imply higher feeding rates in bolder individuals, as they eat more food than subordinate ones (Ahvenharju & Ruohonen, 2006; Gherardi & Daniels, 2003) and have higher functional responses (Hartley et al., 2019). The crayfish in our studies have been kept in isolation to exclude such dominance effects (Moore, 2007). However, it could be that lower feeding rates are retained even in the absence of competition. For example, subordinate threespined sticklebacks (Gasterosteus aculeatus) chose the inferior diet even in the absence of dominant individuals (Milinski, 1982). Thus, the rank of each tested individual in a prior dominance hierarchy among the individuals might have reflected their consumption rates.

The locomotor crossover hypothesis states that predators exhibiting higher activity levels consume more prey when preying on low-activity prey (Huey & Pianka, 1981). However, we could not find these correlations for *a* and *h*. We observed that faster moving crayfish were often not foraging but running along the aquarium pane, thereby ignoring mussels on their path. Activity, as we measured it, might not accurately reflect foraging activity, and periods of real foraging activity should be better distinguished from non-feeding activities to find the presumed positive links shown for other species (e.g. McGhee et al., 2013; Pruitt et al., 2011; Toscano & Griffen, 2014).

5 | CONCLUSIONS

The link of certain behavioural types with food consumption is probably not consistent across contexts but depends on the way these traits are measured. We could, however, demonstrate that marbled crayfish and spiny-cheek crayfish differ in their functional response and in several parameters related to their feeding behaviour on mussels. Our detailed account of feeding parameters was able to mechanistically predict real consumption rates, and our data suggest stronger effects of spiny-cheek crayfish on mussel prey. However, if we look at the invasion history and population development of the invasive Dreissena mussels and the invasive spiny-cheek crayfish, we believe that crayfish cannot substantially reduce the mussels in most invaded systems. We further provide important data on the trophic ecology of marbled crayfish which still are at an early stage of invasion. Both the spiny-cheek crayfish and marbled crayfish are in the List of Invasive Alien Species of Union Concern (EU Regulation 1143/2014), banning the trade with these species and enforcing monitoring and management. The few systems that have confirmed self-sustaining populations of marbled crayfish seem to favour sympatry of both species (Chucholl & Pfeiffer, 2010; Chucholl & Wendler, 2017), and communities with multiple crayfish will probably increase in number. High longterm consumption, interspecific aggression (and low intraspecific

aggression), and reproduction rates, however, can promote further establishment and spread of marbled crayfish. Thus, known marbled crayfish populations, which are mostly restricted to small lakes (Chucholl, 2015), should be monitored and contained, as combined effects on ecosystems might be additive or even amplified (Jackson et al., 2014). Finally, behaviours in general are an integral part of biodiversity and essential to conservation but have not yet received much attention (Cordero-Rivera, 2017). Marbled crayfish will therefore bring a change to European aquatic systems that might be less obvious.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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