Habitat complexity reduces feeding strength of freshwater predators

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LF and JR designed the study, with support by AL and BCR. LF conducted the experiment. BCR, MA, JR, AL, IdG, and LF analysed the data. MA, LF, IdG, AL, AE drafted the manuscript, and all the authors provided feedback, contributed to the writing and gave final approval for publication.

Abstract

The physical structure of an environment potentially influences feeding interactions among organisms by providing refuges for prey. We examined how habitat complexity affects the functional feeding response of an ambush predator (damselfly larvae *Ischnura elegans*) and a pursuit predator (backswimmer *Notonecta glauca*) feeding on the isopod *Asellus aquaticus*. We run experiments in aquatic microcosms with an increasing number of structural elements (0, 2, or 3 rings of plastic plants in different spatial configurations), resulting in five habitat complexity levels. Across these levels, predators were presented with different prey densities to determine their functional response. The experimental design and statistical analysis allowed us to test for effects of structure presence, amount, and complexity level on functional response in one pass, without confounding predictors. The feeding for both predators across all complexity levels was best described by a Type II functional response model and habitat drove feeding strength. Regarding the latter, the predators showed different responses to the complexity treatments. The overall feeding rate of *I. elegans* was mainly driven by the absence vs. presence of structure. Yet, in the case of *N. glauca* feeding rate was strongly dependent on habitat complexity with the predator showing unique maximum feeding rates (i.e. the inverse of the handling time) for each complexity level and a decreasing attack rate with increasing amount of habitat. Overall, prey consumption was less than half for both predators when complex structures were present, compared to the no habitat structure environment. Our findings demonstrate that habitat complexity dampens feeding rates and therefore plays a key role in the stability of freshwater ecosystems.

Keywords: habitat complexity, functional response, trophic interactions, predation. stability

Introduction

The physical structure of an environment is a crucial factor in shaping community composition and the ecological processes driven by living organisms. Habitat complexity has been shown to influence population density, body size, and species richness of invertebrates in both terrestrial and aquatic ecosystems (Flores et al. 2016, White and Walsh 2020, Soukup et al. 2022). Furthermore, habitat complexity is also likely to influence the interactions among organisms by providing more refuge, thereby reducing predation risk for prey (Hauzy et al. 2010, Vucic-Pestic et al. 2010, Vucic-Pestic et al. 2010, Orrock et al. 2013, Barrios-O'Neill et al. 2015). Indeed, previous studies have demonstrated that increasing habitat complexity can lower predation pressure on prey, thus reducing the top-down control exerted by predators (Kalinkat et al. 2013, Mocq et al. 2021, Chang and Todd 2023). Yet habitat complexity could also aid predators in their search for prey, particularly those operating in three-dimensional environments (Pawar et al. 2012), as observed in the case of a freshwater copepod preying on ciliates (Reiss and Schmid-Araya 2011). Therefore, habitat complexity can potentially modify or shape energy flows through food webs, influencing feeding relationships between resources and consumers and among predators and prey.

In general, feeding rates are determined by the time required for predators to find, attack, capture, handle, and ingest their prey (Holling 1959a, 1959b). Testing how refuge availability and habitat complexity alter trophic relationships requires careful experimental design to avoid confounding the amount of structure with habitat complexity (St. Pierre and Kovalenko 2014, Flores et al. 2016). For instance, performing a laboratory experiment, Kalinkat et al. (2013) attributed the observed changes in feeding rates to a dilution effect (i.e. higher amount of structure, leaves in that case, had a dilution effect on prey density) and observed that attack

rates by the predator did not change per unit surface. Nevertheless, complexity can also increase through changes in the arrangement of a fixed number of structures rather than simply adding more, which must be considered in experimental designs.

Functional response models are a suitable tool when it comes to addressing the effects of habitat complexity on species interactions, as they describe the relationship between prey density and the intake of prey by a predator (Holling, 1959a, b). The feeding rate usually follows either a hyperbolic or s-shaped (sigmoidal) relationship with increasing prey density (see e.g. (Kalinkat et al. 2023), also known as Type II and Type III functional response, respectively (we describe the models in the methods section, also see (Rall et al. 2025).

The hyperbolic shape of a type II functional response is determined by an initial increase of the feeding rate, driven by the search speed (a.k.a. attack rate, capture rate, filtration rate, and others) and the handling time, which controls satiation of the response (Holling 1959a). In the case of a type III functional response (Holling 1959a), the attack rate itself is a function of prey density, which is either linear or a power law function (Jeschke et al. 2002, Vucic-Pestic et al. 2010, Kalinkat et al. 2013, Pritchard et al. 2017, Rosenbaum and Rall 2018, Juliano et al. 2022, Rall et al. 2025). In fact, habitat complexity has been put forward as driving a type III response (Vucic-Pestic et al. 2010, Vucic-Pestic et al. 2010, Kalinkat et al. 2013, Barrios-O'Neill et al. 2015).

In addition to habitat complexity, the predation strategy of the predator is an important factor determining the interaction strength and by extension the stability of food webs (Almany 2004, Schmitz 2017). These strategies include "ambush" (also known as "sit-and-wait" tactics) and "pursuit" (active chasing), and these traits can determine spatial utilization and interactions with environmental structures (Pawar et al. 2012, Schmitz 2017). For instance, ambush

predators, exemplified in aquatic systems by species like dragonfly and damselfly nymphs, occur in complex habitats that provide ample hiding spots, enhancing their ability to remain concealed and ambush prey (Mocq et al. 2021, Soukup et al. 2022, Chang and Todd 2023). Conversely, pursuit predators, such as predatory fish, certain types of predatory shrimp or backswimmers require more open and less obstructed spaces to effectively chase down their prey and dense structures within complex habitat can impede their navigation and reduce hunting efficiency (Almany, 2004; Warfe & Barmuta, 2006). Consequently, habitat complexity is likely to have varying impacts on predatory success depending on the predator's hunting strategy. For instance, in aquatic environments, a more complex habitat may favour ambush predators by providing increased hiding opportunities, while posing challenges for active swimming predators, thereby potentially reducing their hunting efficiency(Almany 2004, Dunn and Hovel 2020, Froneman and Cuthbert 2022). Studying how functional response of different predators responds to habitat structure is crucial to understand trophic interactions and energy transfer through real food webs in nature.

Our aim was to explore how two different predators with contrasting hunting strategies are affected by habitat complexity in their search and consumption of prey. Specifically, we tested how habitat complexity (measured as (1) the presence of structure, (2) the amount of structure and (3) the spatial arrangement of structure) influenced the functional response parameters, addressing three hypotheses:

1. Habitat complexity alters the shape of the functional response curve, as more structure can create refuges for prey and makes detection of prey more challenging, particularly at low prey densities.
2. Feeding rates generally decrease with increasing amount of habitat structure resulting in altered functional response parameters.

3. The pursuit predator (*N. glauca*) will show a different response to habitat structure compared to the ambush predator (*I. elegans*).

Material and Methods

Experimental set-up

The experiment was carried out using individual microcosms (9.5 cm diameter and 11.5 cm high circular beakers). The prey (water hog-louse *Asellus aquaticus*) was provided with leaves to feed on. Hence, air-dried alder leaves (*Alnus glutinosa* L.) were weighed, added to each microcosm (2 g each) and conditioned in 500 mL water (1 part of filtered pond water to 5 parts of tap water) for 7 days. The water was renewed when the prey was introduced to the microcosms. Every microcosm was served by one air-stone, and it was sealed with cling film to prevent evaporation. The experiment was run in a controlled-temperature room (15 ºC) with a 14 h light:10 h dark cycle.

When manipulating habitat complexity, it was important to disentangle the effects of complexity *per se* from the effects of amount of structure in the microcosm (see Kalinkat et al. 2013 for reasoning). We used plastic rings to create both structure and different levels of complexity. These rings were artificial plastic plants mimicking the aquatic plant *Ceratophyllum* spp. (Code No. FRF 491, Fish are Fun®). Habitat complexity was created in three ways: 1. as the presence vs. absence of habitat structure; 2. as the amount of structure (0, 2 or 3 of plastic plant rings); and 3. as two spatial configurations of structures in the case of 2 and 3 rings (see Figs. 1&2 and Flores et al. 2016), resulting in 5 complexity levels. The order

of these five levels (from ‘simple’ to ‘complex’ [levels 0, 1, 2, 3 and 4] was determined by measuring the fractal dimension in the feeding arena (see Flores et al. 2016).

Feeding functional response

We tested the feeding functional response of the ambush predator *Ischnura elegans* (van der Linden) (16.8 mm average length and 3.5 mm average head width) and a pursuit predator *Notonecta glauca* (L.) (14.7 mm average length and 4.9 mm wide) preying on *Asellus* (6.6 mm average body length).

The predators were able to get into the structures added to the microcosms, which thus, did not function as a full refuge for prey. The predators were allowed to feed for 24 hours. We used time blocks to run a replicate each, which were all started two days apart from each other because of the time needed to sort *A. aquaticus* individuals. Further, the blocks had the advantage that this approach allowed us to adjust the very high densities after running the first replicate and to further adjust the number of replicates needed after observing feeding during the first time block. Prey densities for *I. elegans* were 1, 3, 5, 10, 30, 80 and 120 individuals per microcosm. Prey densities for *N. glauca*, were 1, 3, 5, 10, 30, 80, 120 and 180 individuals per microcosm 1, 3, 5, 10, 30, 80, 120, and 180 individuals per microcosm. In total we run 297 microcosms. The data are available in Flores et al. (2025)(Flores et al. 2025).

Data Analysis

We first investigated if the shape of the functional response was a hyperbolic type II or s-shaped type III for all ten combinations of complexity treatment and predator species. This was achieved using a phenomenological test (Pritchard et al. 2017, Juliano 2020) and validated by fitting a so-called generalized functional response model allowing for a smooth shift between

type II and type III functional responses (Rosenbaum and Rall 2018). A full supplemental statistics report (Rall et al. 2025) and the code are available.

Holling (1959a) described the mechanics of predation mathematically:

$$F = \frac{aN}{(1+aT_hN)}$$

where the feeding rate, F, is a hyperbolic function in which the attack rate, a, drives the initial T_h slope, and the handling time, h, controls the satiation and N is the density of prey. While we discuss and explain all data analysis in-depth in Rall et al. (2025), it is worth noting that, as an 'updated approach' to Holling, the generalized functional response model (Real 1977, Williams and Martinez 2004, Vucic-Pestic et al. 2010, Rosenbaum and Rall 2018) is:

$$F = \frac{F_{max}N^{1+q}}{N_{half}^{1+q}+N^{1+q}} = \frac{bN^{1+q}}{1+bT_hN^{1+q}} \qquad (1)$$

where the feeding rate F depends on the prey density N. F_{max} is maximum feeding rate (Real 1977), N_{half} is the half saturation density (Real 1977), T_h is the handling time (Holling 1959b), b is the attack coefficient (Vucic-Pestic et al. 2010) and q is the shape parameter (Williams and Martinez 2004, Vucic-Pestic et al. 2010, Rosenbaum and Rall 2018). If q is „0", the function becomes a type II functional response (Holling 1959b), and if q is (significantly) greater than „0", the function becomes s-shaped with $q = 1$ being a 'strict' type III functional response often used if analyzing functional response experiments (e.g. Kalinkat et al. 2023). We will refer to the models with the parameters attack coefficient and handling type as Holling type of functional response, and with the parameters maximum feeding rate and half saturation density as Real type of functional response. Both versions can be translated into each other by

$$F_{max} = {}^{1}/_{T_h} \text{ and } N_{half} = {}^{1}/_{(bT_h)^{1/1+q}} \qquad (2).$$

The attack rate a, which is often used in functional response analyses is a function of prey density if $q > 0$ and can be described by $a = bN^q$ (Vucic-Pestic et al. 2010). The attack rate, a, becomes the attack coefficient b if $q = 0$ (Type II functional response).

After determining the shape of the functional response, we tested a suite of functional response models to address habitat effects on the functional response parameters (see the supplemental statistical report, Rall et al. 2025, for details). This suite of models tested for 1) the assumption that habitat does not influence feeding, 2) an effect of no structure vs. structure, 3) for an effect caused by the amount of structure and 4) for effects due to the complexity of the structure (while being related to 'amount'). The models targeted two parameters (case type II or strict type III) or three parameters (case generalized functional response) at once (Table 1). We dubbed the former 'Holling' and the latter 'Real' as these authors were the first to introduce these parameters (Holling 1959a, 1959b, Real 1977). Testing four assumptions on two parameters (type II and strict type III functional response) in a fully factorial fashion gives a suite of 16 models for the 'Holling' (1H to 16H) and the 'Real' type (1R to 16R) of functional responses each (Table 1). Consequently, models 1R to 16R targeted F_{max} and N_{half} (Real type) and models 1H to 16H targeted parameters T_h and a. In case we detected any type III functional response (see above) the full-factorial scheme would need 64 models for each functional response formulation (see the supplemental statistics report, Rall et al. 2025, for details).

This approach allowed testing for these different habitat predictors on all functional response parameters in one pass and avoided confounding 'amount of structure' with 'complexity', based on the rationale developed in Flores et. al. (2016). We compared the models by using both the Akaike's Information Criterion (AIC) and the Bayesian information criterion (BIC), where the lowest AIC and BIC indicates the best (most parsimonious) model. The output includes a point estimate for the parameter and lower and upper confidence intervals (CIs).

Hence, the functional response models provide information about the overall amount of prey eaten, driven by the maximum feeding rate or its inverse, the handling time. This effect is most obvious at high prey densities where the curve reaches its asymptote. The attack rate, and the half saturation density predominantly control the feeding rate at lower densities, and we were able to compare those parameters between habitat treatments.

Results

The shape of the functional response curves for both *N. glauca* and *I. elegans* consistently fit best to a type II model for all five complexity levels and this result held for both the classical phenomenological test and for fitting the generalized functional response model directly to data (see Supplementary Information Tables 1 and 2).

Therefore, we tested a total of 32 type II functional response models (Table 1) to test for the effect of 'habitat'. For the functional response exhibited by *Ischnura elegans*, the best fitting model (both lowest AIC and BIC, Table 2) was 'model 5R' (Table 1, Figure 1). This model assumed that the effect of structure presences vs. absence overrides all other possible predictors. In the '5R' model, F_{max} takes a value of 28 prey eaten in 24 h when no structure is present (CI: 19.4 to 40.8). However, when structure is present, then F_{max} is 14.6 (CI: 10.7 to 29). N_{half} is not affected by the habitat and takes the value of 57 prey items per arena (CI: 34 to 94).

The best fitting (most parsimonious) model (both lowest AIC and BIC) for *Notonecta glauca* was 'model 15H' and this model assumed that each complexity level has a unique handling time, T_h, and that attack rate, a, decreases with increasing amount of habitat structure. Hence, the parameters that affect feeding rate are more complex in this case. Maximum feeding rate (from the handling time ($F_{max} = {}^{1}/_{T_h}$)) was 31 (CI: 26 to 35) prey eaten in 24 h for complexity level 0 (no structure, level 1), 18 (CI: 15-21), for level 2, 28 (CI: 24-33), 21 (CI: 17 to 27) for level 3 and 19 (CI: 15 to 23) for level 4.The attack rate decreased with increasing number of habitat structural elements (rings, $log_{10}(a) = a_{intercept} + a_{slope}N_{rings}$), indicated by a negative slope (-0.144, CI: -0.191 to -0.097).

The reason why this more complex model was significant (for the maximum feeding rate) over the very similar, but simpler, ‘presence of structure’ model, was that ‘unexpected’ responses were observed when two plastic plant rings had been added to the microcosms (Figure 3). A possible explanation is that the configuration of 2 rings into two different shapes creates very different habitat types and that this is not the case when three rings were used (the latter essentially created an ideal hiding spot in an any case, a ‘dense ball’). For two rings, it is likely that one of the configurations left more space for the agile pursuit predator *Notonecta* to navigate in.

Overall, fitting these models showed that the amount of prey eaten was generally higher without habitat compared to all high habitat complexity levels. On average, prey consumption was less than half for both predators when complex structures were present, compared to the no habitat structure environment. Both predators consumed significantly more prey in the absence of structures, with average consumption reaching 5-6 times their body weight in 24 hours.

Discussion

Our findings suggest that habitat complexity affects predator-prey interactions in freshwater ecosystems. Results from our feeding experiments showed that feeding, i.e. the functional response type, did not significantly vary with habitat complexity (all feeding was consistent with a type II response). However, we found support for the hypothesis that increased habitat complexity would decrease feeding rates overall. Both, ambush predator (damselfly larvae *Ischnura elegans*) and pursuit predators (backswimmer *Notonecta glauca*) showed higher

feeding rates in microcosms without structures compared to those with structure. This suggests that while habitat complexity reduced feeding rates by affecting maximum feeding rate, attack rate and handling time, the overall mechanisms (shape of the functional response curve) remained consistent across different complexity levels.

Generally, it is known that complex structures offer refuge for prey, thereby reducing the efficiency of predators (Hauzy et al. 2010, Mocq et al. 2021, Froneman and Cuthbert 2022). This reduction in feeding rates due to increased habitat complexity implies a decrease in the top-down control of predators on prey populations(Chang and Todd 2023). In our study, the reduction in feeding rates was associated with both a reduction in attack rate and an increase in handling time (i.e. an increase in maximum feeding rate while the half saturation density is relatively constant). However, the magnitude of these changes varied across different complexity levels. Previous studies, conducted using microcosm approaches, have shown that attack rate and handling time can respond differently to habitat complexity. For instance, a study on zooplankton prey *Aracartia longipatella* and predator *Mesopodopsis wooldridgei* reports stronger effects on attack rates (Froneman and Cuthbert 2022); while the dragonfly larvae *Aeshna cyanea* preying on *Chaoborus obscuripes* larvae changes handling time with complexity (Mocq et al. 2021). Soil mites preying on collembolans displayed varying response in both attack rate and handling time with habitat structure (Hauzy et al. 2010).

We hypothesized that at lowest habitat complexity (i.e. microcosms without added structures), the shape of the functional response would best fit to a type II functional response, because feeding rates would be mainly limited by the time required by the predator to kill and eat its prey. With increasing habitat complexity levels, we expected sigmoid functional response (i.e. type III functional response), as at low prey densities the efficiency of the predator would be limited by the structures offering multiple hiding places (Vucic-Pestic et al. 2010a,b,

Kalinkat et al. 2023). However, as prey density increases and the amount of refuge become saturated, the efficiency of the predator would again increase at intermediate prey densities. Nevertheless, functional response of both predators was consistently best described by a type II model across all the levels of habitat complexity. For *Ischnura*, (Mikolajewski et al. 2015) highlighted a phenotypic plasticity, allowing it to adapt to environmental changes while maintaining a Type II functional response. Moreover, our design of the habitat structure allowed both predators to enter the potential prey refuge which may be also a reason for not finding a type III response. One prey per predator was the lowest density in our experiment, which corresponds to a density of 141.1 individuals per square metre, but in nature, lower abundances, can be observed for many taxa (Larrañaga et al. 2009). Indeed, not considering low prey in laboratory set-ups can hinder the detection of a type III response (Sarnelle and Wilson 2008). Although the prevalence of type III functional response has been postulated as the way to maintain stability of prey populations and high diversity (Murdoch and Oaten 1975, Rall et al. 2008, Kalinkat et al. 2023), type II is still the most common functional response in previous studies (Dunn and Hovel 2020).

Although the type III functional response was not supported by our data, we saw a hint that the interaction of both predators and its prey was stabilizing as feeding rates generally decreased with the presence and with increasing complexity of the habitat structure. The general decrease of interaction strength is associated with more stable population dynamics and higher species richness in model food webs (May 1972, Yodzis and Innes 1992, Rall et al. 2008).

The two predators in our experiment differed in terms of their predatory strategies and the functional response parameters highlighted some of those differences. The pursuit predator (the backswimmer *N. glauca*) exhibited three times the attack rate of the ambush predator (the damselfly *I. elegans*), although a similar handling time when no structures were present in their

environment. Also, as an open-water hunter, *N. glauca* is more likely to operate in a 3D environment compared to *I. elegans* that sits within/ on habitat surface (see Pawar et al. 2012). Indeed, dimensionality of consumer search space is probably a major driver of species coexistence, and the stability and abundance of populations (Pawar et al. 2012). As predicted, the effect of habitat complexity was stronger for the pursuit predator than the ambush predator. An explanation is the barrier effect that the structures can create for the pursuit predator, reducing the visibility of prey and the capture success(Grabowski and Kimbro 2005). In agreement with(Svensson et al. 2000), habitat heterogeneity significantly reduced predation efficiency in *N. glauca* by providing refuges that lower prey visibility and decrease attack rates, highlighting the vulnerability of pursuit predators to habitat complexity. Previous studies have also shown that *Notonecta* spp. are more successful in open environments(Gittelman 1974), and that factors such as water depth and refuge availability influence its hunting behaviour (Cockrell 1984).

Our short-term experiment with three species certainly demonstrated that habitat complexity is an important factor to be considered when it comes to trophic interactions. Both predators were more successful in environments without structure and were able to feed on substantially more prey without structure.

Conclusion

We conclude that habitat complexity has the potential to shape species interactions and carbon flow within the food web. The results of this study demonstrate that increased habitat complexity significantly reduces feeding rates in both *Ischnura elegans* and *Notonecta glauca*. The reduction in predation efficiency, driven by decreases in attack rates and increases in handling times, supports the idea that structural complexity provides refuges for prey, limiting

predator success. Despite these changes in feeding rates, both species maintained a Type II functional response across all levels of habitat complexity, indicating that while habitat structure affects predator efficiency, it does not fundamentally alter the shape of the functional response curve. Overall, these findings underscore the critical role of habitat complexity in shaping trophic interactions and sustain energy flow. In more complex, natural ecosystems, habitat complexity will likely drive species coexistence, stability of food webs and diversity of communities.

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Tables

Table 1: Overview of models tested on 2 parameters at once to show if the feeding rate was affected by habitat complexity. Four parameters are tested, yet only 2 of them in one pass as this reduced the testing from a possible 128 combinations to 32 models. Also, the two parameters correspond to different simulation models (after Real 1977 and Holling 1959 respectively). Levels (used to calculate df of the models) are for hypothesis: One: presence has effect—2 levels (present and absent); Two: amount has effect—3 levels, zero, 2 and 3 plastic plant rings and Three: complexity level (fractal dimension) has effect —5 levels: 0-4.

	'Holling (1959) approach'									'Real (1977) approach'							
Parameter	T_h				***a***					F_{max}				N_{half}			
Hypothesis	**zero**	**one**	**two**	**three**	**zero**	**one**	**two**	**three**		**zero**	**one**	**two**	**three**	**zero**	**one**	**two**	**three**
	habitat has no effect	presence has effect	amount has effect	complexity level has effect	habitat has no effect	presence has effect	amount has effect	complexity level has effect		habitat has no effect	presence has effect	amount has effect	complexity level has effect	habitat has no effect	presence has effect	amount has effect	complexity level has effect
Model									**Model**								
1H	1	0	0	0	1	0	0	0	1R	1	0	0	0	1	0	0	0
2H	1	0	0	0	0	1	0	0	2R	1	0	0	0	0	1	0	0
3H	1	0	0	0	0	0	1	0	3R	1	0	0	0	0	0	1	0
4H	1	0	0	0	0	0	0	1	4R	1	0	0	0	0	0	0	1
5H	0	1	0	0	1	0	0	0	5R	0	1	0	0	1	0	0	0
6H	0	1	0	0	0	1	0	0	6R	0	1	0	0	0	1	0	0
7H	0	1	0	0	0	0	1	0	7R	0	1	0	0	0	0	1	0
8H	0	1	0	0	0	0	0	1	8R	0	1	0	0	0	0	0	1
9H	0	0	1	0	1	0	0	0	9R	0	0	1	0	1	0	0	0
10H	0	0	1	0	0	1	0	0	10R	0	0	1	0	0	1	0	0
11H	0	0	1	0	0	0	1	0	11R	0	0	1	0	0	0	1	0
12H	0	0	1	0	0	0	0	1	12R	0	0	1	0	0	0	0	1
13H	0	0	0	1	1	0	0	0	13R	0	0	0	1	1	0	0	0
14H	0	0	0	1	0	1	0	0	14R	0	0	0	1	0	1	0	0
15H	0	0	0	1	0	0	1	0	15R	0	0	0	1	0	0	1	0
16H	0	0	0	1	0	0	0	1	16R	0	0	0	1	0	0	0	1

1= model tests for this, 0= model does not test for this

Table 2: The six best models that describe the functional response parameter F_{max} and N_{half}; and T_h and a, for predators *Ischnura elegance* and *Notonecta glauca*. The full suite of models can be found in Rall et al. (2025). The best fit of the models was tested using AIC (AIC generally performs better for models that have more parameters) and BIC. A low value indicates the best fit.

AIC			**BIC**		
Model	**df**	**dAIC**	**Model**	**df**	**dBIC**
Ischnura elegance					
Model 5R	**3**	**0.000**	**Model 5R**	**3**	**0.000**
Model 7R	4	0.265	Model 5H	3	1.583
Model 6H	4	0.952	Model 7R	4	2.731
Model 6R	4	0.952	Model 6H	4	3.418
Model 5H	3	1.583	Model 6R	4	3.418
Model 13R	6	2.107	Model 7H	4	4.718
Notonecta glauca					
Model 15H	**7**	**0.000**	**Model 15H**	**7**	**0.000**
Model 16H	10	1.274	Model 9R	3	1.004
Model 16R	10	1.274	Model 11H	4	1.485
Model 15R	7	1.990	Model 11R	4	1.485
Model 14R	7	4.189	Model 13R	6	1.507
Model 13R	6	4.854	Model 15R	7	1.990
Model 12H	7	8.352	Model 7H	4	2.516

Figure captions

Figure 1. Functional response curves for the ambush predator *I. elegans* for microcosm without structure and with structure (plastic plants).

Figure 2. Functional response curves for the pursuit predator *N. glauca* for each habitat complexity level (a-e are levels 0 to 4 respectively). Habitat complexity levels 1 and 2 (b, c) were created with two rings of plastic plants, while levels 3 and 4 (d, e) had three rings of plastic plants.

Figure 3. The functional feeding response parameter F_{max} of *Notonecta glauca* feeding on *Asellus aquaticus*. Amount of structure (number of plastic plant rings) is regressed against the feeding rate, and this shows that when two rings are added, there is an 'unexpected response' explaining why a more complex model that assumed an effect of fractal dimension is more parsimonious.

Figures

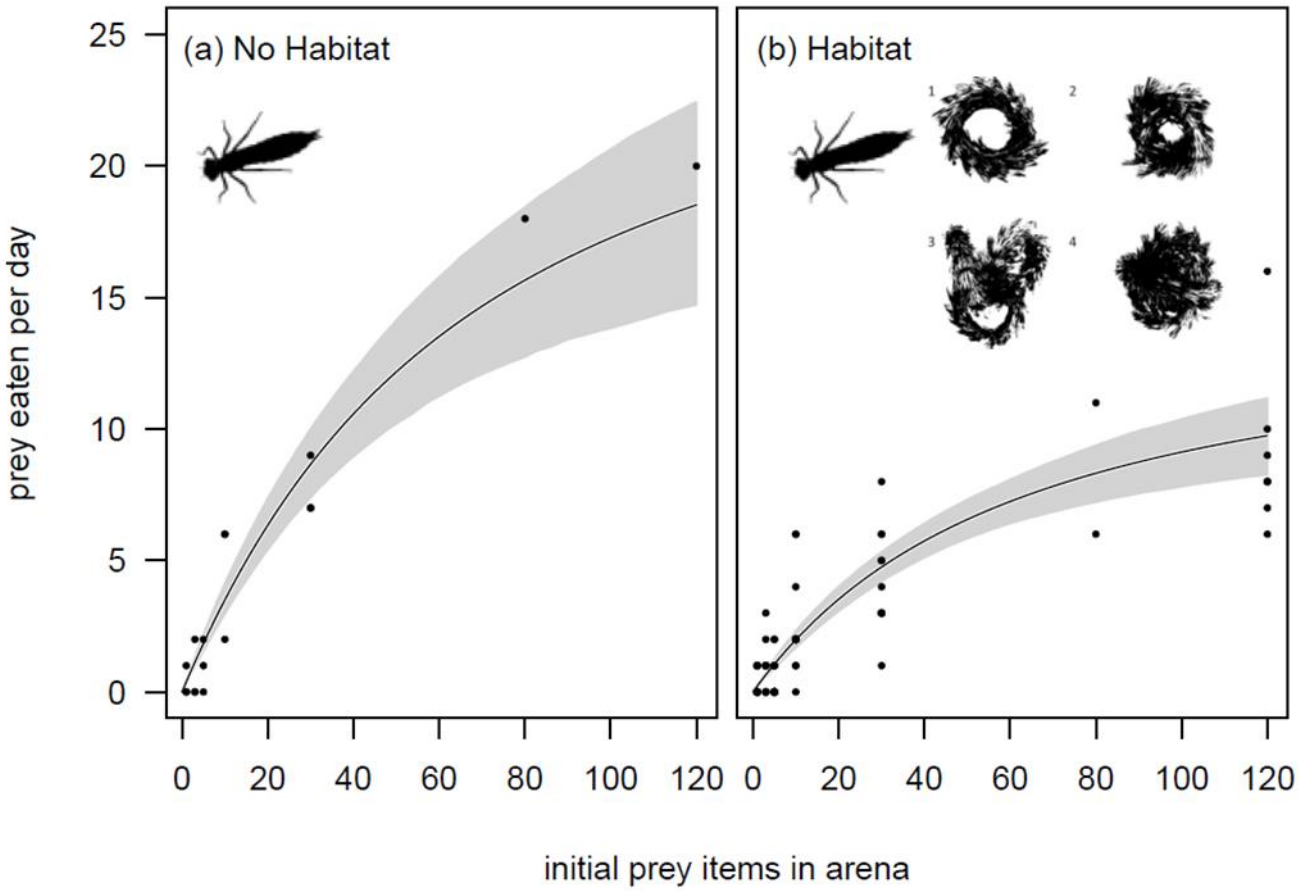

Figure 1

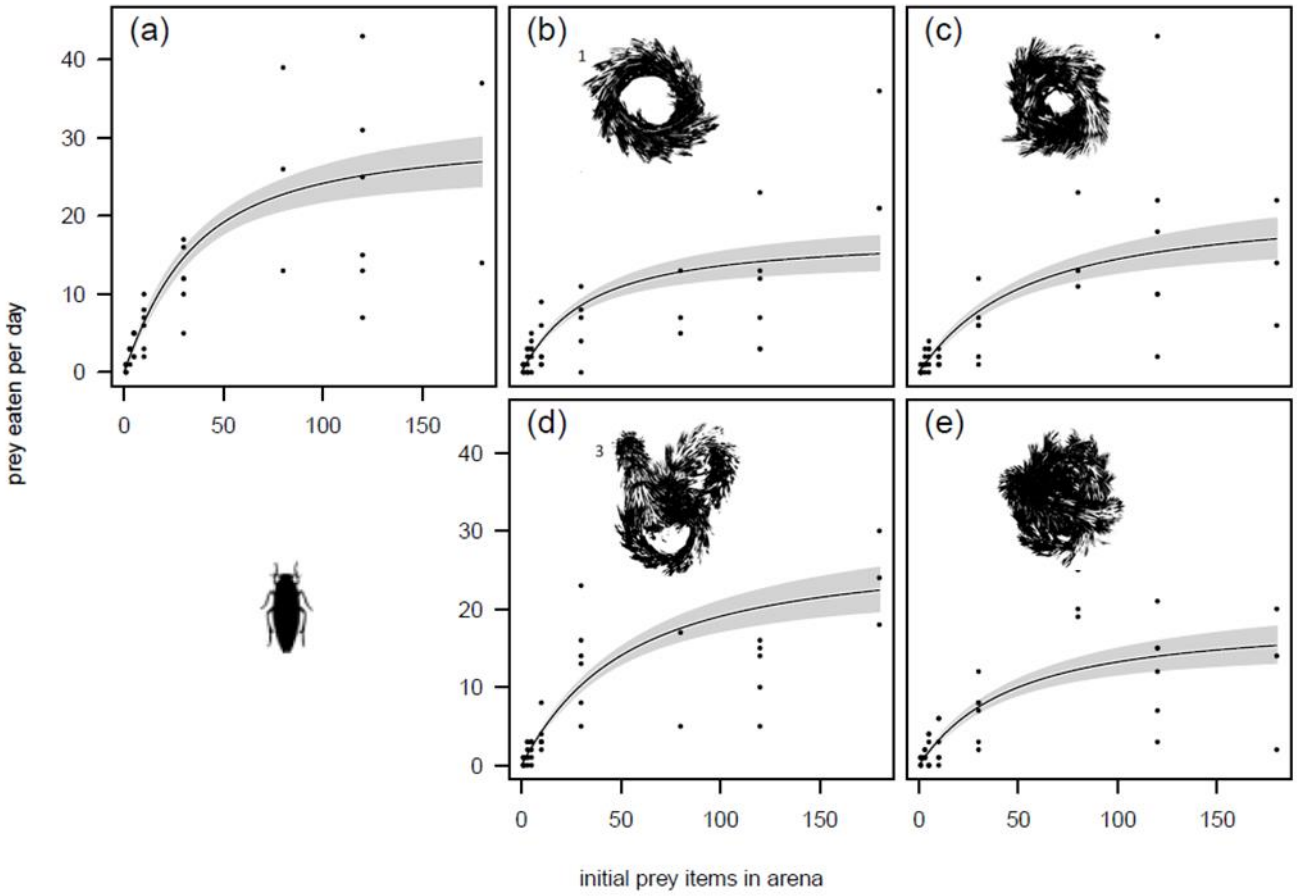
(a)
(b)
(c)
(d)
(e)
prey eaten per day
initial prey items in arena
0
10
20
30
40
0
50
100
150

Figure 2

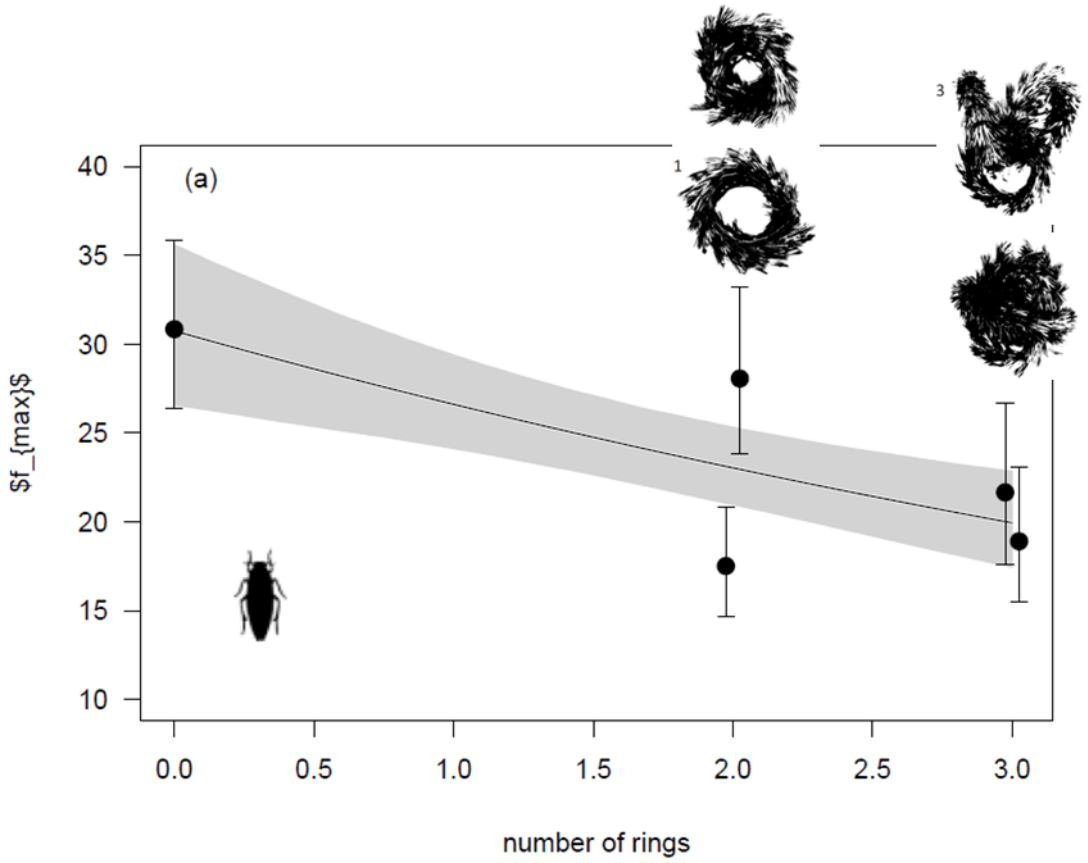

Figure 3

Supplementary Information

The full data and statistics can be found here:

1. Flores, L., J. Reiss, A. Larrañaga, B. C. Rall, M. Aranbarri, and I. de Guzmán. 2025. Complexity reduces feeding strength of freshwater predators (CRITTER) - Data. https://doi.org/10.5281/ZENODO.14891981

2. Rall, B. C., Aranbarri, M., Flores, L., de Guzmán, I., Larrañaga, A., & Reiss, J. (2025). Complexity reduces feeding strength of freshwater predators (CRITTER) - Supplemental Statistics Report. Zenodo. https://doi.org/10.5281/zenodo.14898819

3. GitHub Repository: https://github.com/b-c-r/CRITTERstatistics

SI Table 1: Testing for functional response type for two predators feeding at 5 complexity levels (0 to 4), fitting a Polynomial to Proportion Feeding. The functional response pattern consistently fits a type II pattern. Testing for functional response type using 'Juliano approach'. We observed a declining proportion of eaten prey consistent with a type II functional responses (i.e. both a negative linear and a positive quadratic term. There were three exceptions of this pattern – at the highest complexity level, the results for I. elegans suggest a hump shaped functional response pattern as the linear term is positive and the quadratic term is negative. However, both estimates are not significant. Further, the N. glauca functional response for complexity levels 3 and 4 show a negative quadratic term, which could be indicative of a type III functional response, yet both results are not significant.

Predator	Complexity	Linear (Q)	Quadratic (Q)	Linear (L)	Type
Ischnura elegans	0	-(n.s.)	-(n.s.)	-(*)	II
Ischnura elegans	1	-(n.s.)	-(n.s.)	-(*)	II
Ischnura elegans	2	-(n.s.)	-(n.s.)	-(***)	II
Ischnura elegans	3	-(n.s.)	-(n.s.)	-(**)	II
Ischnura elegans	4	-(n.s.)	-(n.s.)	-(**)	II
Notonecta glauca	0	-(***)	-(***)	-(***)	II
Notonecta glauca	1	-(***)	-(***)	-(***)	II
Notonecta glauca	2	-(***)	-(**)	-(***)	II
Notonecta glauca	3	-(n.s.)	-(n.s.)	-(***)	II
Notonecta glauca	4	-(*)	-(n.s.)	-(***)	II

SI Table 2: Testing for functional response type using q-exponent (known as Hill exponent) approach. The significance of the shape parameter q of all ten separately fitted generalized functional response models. None of the q values is significantly different from zero, hence the feeding rate follows a functional response type II, confirming results from SI Table 1.

Predator	**Complexity**	q	Significance	**Type**
Ischnura elegans	0	0.116	n.s.	II
Ischnura elegans	1	0.047	n.s.	II
Ischnura elegans	2	-0.001	n.s.	II
Ischnura elegans	3	-0.001	n.s.	II
Ischnura elegans	4	0.193	n.s.	II
Notonecta glauca	0	-0.011	n.s.	II
Notonecta glauca	1	-0.006	n.s.	II
Notonecta glauca	2	0.194	n.s.	II
Notonecta glauca	3	-0.002	n.s.	II
Notonecta glauca	4	-0.001	n.s.	II