



FEATURE ARTICLE



# Handling- or digestion-limited predators: the role of body mass and habitat complexity in predator functional response

Nan Hu<sup>1,2,3</sup>, Yajuan Huang<sup>2</sup>, Zhenglin Yu<sup>4,5</sup>, Tao Zhang<sup>1,6,7,\*</sup>, Dapeng Liu<sup>2</sup>,  
Marcus Lee<sup>3</sup>

<sup>1</sup>CAS Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology,  
Chinese Academy of Sciences, Qingdao 266071, Shandong, PR China

<sup>2</sup>Key Laboratory of Mariculture, Ministry of Education, Ocean University of China, 5 Yushan Road,  
Qingdao 266003, Shandong, PR China

<sup>3</sup>Aquatic Ecology, Department of Biology, Lund University, Lund 223 63, Sweden

<sup>4</sup>Key Laboratory of Coastal Zone Environmental Processes and Ecological Remediation, Yantai Institute  
of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, PR China

<sup>5</sup>Research and Development Center for Efficient Utilization of Coastal Bioresources, Yantai Institute  
of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, PR China

<sup>6</sup>Laboratory for Marine Ecology and Environmental Science, Qingdao Pilot National Laboratory for Marine Science  
and Technology, Qingdao 266237, PR China

<sup>7</sup>Center for Ocean Mega-Science, Chinese Academy of Sciences, Qingdao 266071, PR China

**ABSTRACT:** The predator functional response quantifies the per capita feeding rate of predators as a function of prey density and is a key element of feeding interactions. Variations in its parameters are strongly associated with interaction strength and population dynamics. We examined 18 functional responses within marine whelk–bivalve systems, varying predator body size, prey species, and habitat structure. Our findings suggest that the marine whelk *Rapana venosa* is handling-limited, a predator type that has received less attention in previous research. We propose further categorizing handling-limited predators into 2 types: pursuit-limited (where maximum feeding rate could be influenced by habitat complexity) and ingestion-limited (where maximum feeding rate is impacted not by habitat complexity, but by predator–prey body mass ratios and prey defense strategy). We found that handling time scales negatively with predator–prey body mass ratios, but this trend exhibits layers of complexity. We propose that the transition from handling to digestion limitation with increasing predator–prey body mass ratios underlies this trend. Our study also confirms the importance of prey types, in addition to known effects of body mass ratios and habitat structure. In summary, our study reveals that simple assumptions about body masses and prey de-



A relatively small whelk *Rapana venosa* is feeding on a comparatively large oyster.

Photo: Nan Hu

defense strategy may usefully refine estimates of feeding interactions in complex food webs.

**KEY WORDS:** Feeding interactions · Functional responses · Handling-limited predator · Body masses · Habitat complexity · Prey types · *Rapana venosa*

\*Corresponding author: tzhang@qdio.ac.cn

## 1. INTRODUCTION

Understanding feeding interactions between predators and prey is fundamental to ecology, with direct consequences for predicting population dynamics, food-web stability, and resulting ecosystem functions (Williams & Martinez 2004, Kalinkat et al. 2013, Barrios-O'Neill et al. 2016). Therefore, appropriately characterizing such feeding interactions is essential. The functional response (Holling 1959) is one of the most commonly used frameworks to describe the shape and evaluate the strength of feeding interactions (reviewed by Jeschke et al. 2002). It describes how the per capita feeding rate of predators systematically changes with prey density as a result of the predator's search for, attack, capture, and handling of prey (Holling 1959, 1966, Jeschke et al. 2002).

Despite several models having been developed to capture the mechanistic basis of the functional response, the essential components of search, capture, and handling as outlined by the model of Holling (1959) remain the most popular model. A generalized version of the Holling's disc equation is (Real 1977):

$$N_e = \frac{bN^{q+1}}{1 + bhN^{q+1}} \quad (1)$$

where  $N_e$  is the per capita consumption;  $N$  is the prey density;  $b$  is the search coefficient or capture rate (depending on the scientific field);  $h$  is the handling time that practically represents the time spent subduing, ingesting, and digesting each prey (Jeschke et al. 2002, Sentis et al. 2013); and  $q$  is a scaling exponent that influences the shape of the functional response from a decelerating hyperbola type II ( $q = 0$ ) to a strictly sigmoidal type III ( $q = 1$ ) functional response.

Even though the model characterizes the feeding interaction between predators and prey well, it does not capture the biological processes underlying the functional response (Caldow & Furness 2001, Jeschke et al. 2002). The parameter  $b$  (search coefficient) can be interpreted reasonably, but not the parameter  $h$ , which contains several different biological processes, i.e. pursuing, subduing, ingesting, and digesting the prey (Brose 2010, Sentis et al. 2013). Evidence from empirical experiments highlights that estimates of handling time from models do not always resemble direct observations (Mols et al. 2004, Jeschke & Tollrian 2005, Sentis et al. 2013). Jeschke et al. (2002) demonstrated that the estimate of handling time includes 'digestive pauses', which may drive a longer estimate of  $h$  than empirical observations. Moreover, for many predators, handling and digestion are not mutually exclusive activities, meaning that feeding

interactions can be handling-limited, especially if prey defenses increase. Therefore, Jeschke et al. (2002) proposed that predators are limited by their handling capacity or digestive capacity. The differences between handling-limited and digestion-limited predators have clear implications for predator time allocation strategies, predator hunting modes, and prey defense strategies (Jeschke & Tollrian 2000, Jeschke et al. 2002), and thus it is important to identify predator type in order to understand the mechanisms that underpin and modify handling time. Despite this distinction, most studies have focused on digestion-limited predators, such as fish (Barrios-O'Neill et al. 2015, 2016, Wasserman et al. 2016), crustaceans (Toscano & Griffen 2014, Barrios-O'Neill et al. 2016), and beetles (Vucic-Pestic et al. 2010), although the authors did not mention this term. Studies regarding handling-limited predators are less common (but see Miner et al. 2013, Barclay et al. 2020).

Alongside Holling's disc equation, the  $\frac{3}{4}$  power law scaling of metabolic rate with body mass has become one of the most general theories in ecology, due to metabolism fueling most biological processes. As a result, it provides body mass and its correlates with a central place in models of feeding interactions (Brown et al. 2004, Brose 2010, Kalinkat et al. 2013). For example, the handling time may follow a negative power-law relationship with predator body mass or predator-prey body mass ratios (Vucic-Pestic et al. 2010, Barrios-O'Neill et al. 2016). Given that digestion-limited and handling-limited predators have different time-allocation strategies, this may lead to different relationships between handling time and correlates of biomass. Although it is necessary to consider body mass, it is not sufficient to afford a complete understanding of feeding interactions (Rall et al. 2011, Kalinoski & DeLong 2016). The dimensionality and complexity associated with predator search space can be another essential factor that can systematically modify feeding interactions (Pawar et al. 2012, Barrios-O'Neill et al. 2015, 2016, 2019). For example, complexity in the habitat can provide refugia for prey that would increase predator pursuit time, and therefore constrain their feeding rate. However, handling-limited predators may have a greater ability to search for their prey to compensate for weak handling ability, suggesting that the complexity of habitat may not affect their time-allocation strategy.

In the present study, we aim to provide empirical evidence of such complexity in feeding interactions by fitting several models to quantify systematic effects of predator-prey body mass ratios and habitat complexity on functional response parameters across

different predator–prey feeding interactions. Moreover, we aim to distinguish predator type by comparing estimates and observations of handling time. This framework then allows us to test for relationships between handling time and predator–prey body mass ratios using non-linear least squares regression, as well as to identify the driving factors of handling time based on predator type through linear mixed-effects modeling.

## 2. MATERIALS AND METHODS

### 2.1. Predator and prey species

We used a generalist predatory whelk (*Rapana venosa*), as it is a dominant species in the benthic ecosystem of Laizhou Bay, China (Hu et al. 2016, 2021). It is widely distributed and appears in all types of substrates (Kosyan 2016). This whelk predominantly feeds on bivalves, such as clams, mussels, oysters, and scallops (Harding & Mann 1999, Hu et al. 2016). Small whelks generally attack by drilling through the bivalve shell, whereas large whelks typically feed by using their foot to grasp the prey, without leaving drill-holes (Harding et al. 2007). The 2 strategies for handling prey alters the handling time when dealing with different prey with various anti-predator defenses, which presents the opportunity for the whelk to be either digestion- or handling-limited. Therefore, this special gastropod–bivalve predator–prey system is an excellent model for identifying predator type and parsing handling time of a predator functional response.

We used 3 bivalves that are armored with different defensive strategies as prey: clams (*Ruditapes philippinarum*), which reduce encounter rates with predators by burying themselves in the sediment; scallops (*Chlamys farreri*), which decrease risk by actively jumping to avoid predators; and oysters (*Magallana gigas*), which rely on shell size, morphology, and thickness to reduce the handling efficiency of predators. We assumed that different-sized whelks would allocate time differently to capture these 3 prey, and thus show specific feeding interactions.

### 2.2. Animal collection and maintenance

During May 2016, predatory whelks were collected by SCUBA diving in Laizhou Bay, Bohai Sea (37.3146° N, 119.8209° E), and were transported into the Ecology Laboratory of the Institute of Oceanol-

ogy, Chinese Academy of Sciences, within 2 h. Individual whelks were separated for subsequent experiments, and matched to 1 of 3 size classes (mean wet body mass  $\pm$  SE small = 5.12 g  $\pm$  0.23, medium = 20.79 g  $\pm$  0.37 and large = 58.79 g  $\pm$  2.72). Prey scallops and clams were collected by trapping and dipping from subtidal (36.2749° N, 119.1463° E) and coastal beach (36.2756° N, 119.4377° E) localities, respectively. Oysters were collected simultaneously with the whelks by SCUBA diving. Prey were also sorted, to as closely as possible match a single size class per each prey type (clam = 5.88 g  $\pm$  0.19, scallop = 10.71 g  $\pm$  0.44 and oyster = 31.09 g  $\pm$  1.97). Each species was maintained separately in aerated sea water with associated substrate, at 19°C and 14 h L:10 h D photoperiod. All predators were fed with the clam *Anadara kagoshimensis* for at least 15 d, and starved for 2 d prior to trials.

### 2.3. Experimental design

To fully explore possible combinations in predator and prey body masses, we studied 18 functional responses for 3 sizes of whelks feeding on 3 bivalve prey in 2 substrate types. Experimental trials were conducted in continuously aerated experimental circular arenas (r = 0.5 m, h = 0.4 m) filled with 200 l of filtered (25  $\mu$ m) seawater. Arena treatments were designed to reflect 'simple' and 'complex' habitat types. The simple habitat contained only 100–500  $\mu$ m diameter sand, and complex habitat contained the same sand as simple habitat and 12 black pebbles (14 mm diameter, 5.2 mm tall). For the complex-habitat oyster trials, we used small rocks to which the oysters attached, rather than loose pebbles. Prey were introduced into experimental arenas at 8 densities (2, 4, 6, 8, 16, 24, 32, 48; n = 4 each) 4 h before the introduction of a single starved predator. Four hours was considered enough time for clams to burrow into sand and scallops to hide. Controls were predator-free arenas at all prey densities for both habitats with replication of n = 4. Because trials could be handling-limited functional responses, all trials ran for 96 h to give predators enough time to reach maximum feeding. Trials were ended by the removal of predators, and the surviving prey were enumerated.

### 2.4. Directly measuring handling time

To determine predator type and parse handling time into its components, we conducted trials to directly

measure handling time for all 18 treatment groups. Prey individuals ( $n = 24$ ) were allowed to acclimatize for 4 h, after which a single whelk was introduced. The activity of whelks was recorded using an HD camera (Hikvision, DS-7604N). All trials ran for 2 d to ensure enough time for all predators to complete their first feeding event, as some predators took more than 1 d to consume their first prey, i.e. small whelk–oyster pairs. Handling time was then quantified from these recordings. The handling time here is defined as the time interval from starting the search to the moment when the whelk finished eating, i.e. departing with an open shell and resumption of searching behavior. The time of failure to attack was also counted, i.e. whelks moved away before consuming the prey. There were 6 replicates for each prey species-by-habitat combination.

## 2.5. Functional response model selection and fitting

Eq. (1) assumes that the local prey density does not decline. However, in many experiments, it is unfeasible to keep the prey density constant over time because consumed prey cannot be replaced immediately. To describe the non-replacement of prey experiments, Real (1977, 1979) provided a modified version of Eq. (1):

$$N_e = N_0 \{1 - \exp[bN_0^{q+1}(N_e h - T)]\} \quad (2)$$

where  $N_0$  is the initial prey density,  $T$  is the total experimental time, and the other parameters are the same as in Eq. (1).

More recently, to correctly describe prey depletion during the course of functional response experiments, Rosenbaum & Rall (2018) set up an ordinary differential equation (ODE) by using the generalized Holling's functional response:

$$\frac{dN}{dt} = -\frac{bN^{q+1}}{1 + bhN^{q+1}} \quad (3)$$

The change in prey density  $dN$  over time  $dt$  is more appropriately described by this equation. Parameters here are same as in Eq. (1). This ODE could be more flexible and general to calculate more accurate parameter estimates (Rosenbaum & Rall 2018). For all predator–prey pairs, we used maximum likelihood (Bolker & R Development Core Team 2017) to fit 4 models that included 3 versions of Eq. (2) and the ODE model, Eq. (3). The 3 versions of Eq. (2) were a strict hyperbolic type II functional response ( $q = 0$ ); a

strict sigmoidal type III functional response ( $q = 1$ ); and a general flexible model that allows  $q$  to vary. For the 3 versions of Eq. (2), we used the R package 'frair' (Pritchard et al. 2017) to fit our dataset. For the numerical solution of the ODE model, we used the package 'odeintr' (Keitt 2017), and for the maximum likelihood estimation we used the 'mle2' function in the package 'bbmle' (Bolker & R Development Core Team 2017). We applied the method developed by Rosenbaum & Rall (2018) to solve the ODE and fit our data. All model fitting and statistical analyses were conducted using R 4.3.1.

For the selection of the best functional response model, Akaike's information criterion scores corrected for small sample size (AICc) were used for comparison. Several models exhibited competitive performance as indicated by comparable AICc values. To provide additional clarity, bootstrapping analyses were executed ( $n = 100$ ) to construct confidence intervals around these AICc scores (Table A1 in the Appendix). Consistently, the outcomes of the direct fitting procedures and the bootstrapping analyses were congruent. We used the estimates from the lowest-scoring model. We performed nonparametric bootstrapping ( $n = 2000$ ) for each raw dataset, and we used new datasets to fit the best model to construct 95% confidence intervals and functional response curves (Pritchard et al. 2017).

## 2.6. Distinguishing between digestion- and handling-limited predators

To determine if a predator in the predator–prey pair is digestion-limited or handling-limited, we divided handling time into different components by using the following equation (Jeschke et al. 2002):

$$h = t_{att} + t_{eat} + st_{dig} \quad (4)$$

where  $t_{att}$  is the attack time per prey, defined as the time between an encounter and the end of attack (i.e. from initial contact with the prey to the start of eating), and  $t_{eat}$  is the eating time (the time from capture to the moment when consumption has ended). It is important to clarify that  $t_{eat}$  in this context includes not only the actual consumption of prey tissue but also the time spent drilling a hole in the shell. These actions occur post-capture, during which the whelk keeps its foot wrapped around the prey. Given that no whelk abandoned potential prey after beginning the drilling process, we have classified it under the

eating process.  $s$  is the satiation per prey, defined as the reciprocal of the whole capacity of the gut, and  $t_{dig}$  is the digestion time per prey.  $st_{dig}$  therefore represents the digestive pause that occurs from the end of consumption to the start of a new search. If a predator continues to search for, attack, and consume prey and never reaches satiation, the digestive pause  $st_{dig}$  would be close to 0 (Jeschke et al. 2002). In this case, the predator is handling-limited. In contrast, a digestion-limited predator can reach satiation with digestive pauses ( $st_{dig} > 0$ ). Therefore, we can distinguish the predator type by calculating the  $st_{dig}$  using the estimates minus the direct observations. The  $st_{dig}$  of a digestion-limited predator is significantly greater than 0, while the  $st_{dig}$  of a handling-limited predator is not significantly different from 0. Thus, for each predator–prey pair, we performed a Student’s  $t$ -test to compare the difference between estimates and direct observations (Table A2).

## 2.7. Scaling relationship

After quantifying predator–prey functional responses of 3 size classes of whelks across prey types, we tested for systematic relationships between predator–prey body mass ratios and the handling times across 2 substrates. Predator–prey body mass ratios could be a focal explanatory variable to predator feeding parameters (Barrios-O’Neill et al. 2016). Since our studies included 3 different types of prey species, this allowed us to isolate the effects of predator–prey body mass ratio and translate the output into more general scaling.

We initially compared handling times between 2 habitat structures by using Student’s  $t$ -test. This provided initial justification for pooling handling times ( $t_{34} = 0.052$ ,  $p = 0.959$ ). We transformed both predator–prey body mass ratios and handling times by  $\log_{10}(x + 1)$  to avoid problems at 0. Based on previous studies, predator handling times can be described by an exponentially declining function, which shows exponential declines with predator mass or predator–prey mass ratios (Aljetlawi et al. 2004, Kalinkat et al. 2013, Barrios-O’Neill et al. 2016). We further hypothesized that reductions in handling times would be most pronounced for digestion-limited predators. Moreover, these digestion-limited predator–prey pairs would have high predator–prey body mass ratios. We fitted the following model by using non-linear least-squares regression:

$$\log_{10}(h + 1) = \delta \exp(\epsilon \log_{10}[R + 1]) \quad (5)$$

where  $h$  is the handling time,  $R$  is the predator–prey body mass ratio, and  $\delta$  and  $\epsilon$  are constants.

To determine what factor drives the handling time of predators, we also fitted a linear mixed-effects model with handling time as the dependent variable. Three key predictors were considered: predator–prey body mass ratio, predator mass, and predator type (categorized as either handling-limited or digestion-limited). As these predictors could be highly correlated (all pairwise correlation values of  $R > 0.44$ ), we separately analyzed each in individual models. In each of these separate models, we accounted for habitat complexity, which could also influence handling time, by treating it as a fixed effect. We initially included interaction terms in our models, but these were found to be non-significant (all  $p > 0.052$ ), and thus were subsequently removed. To address potential dependencies within the dataset, including the possibility that observations from the same prey type might not be fully independent (i.e. might share the same avoidance strategy), we included prey type as a random effect in each model. This step allows us to account for the influence of this non-independency on the variance of our response variable, enhancing the reliability of our model results.

## 3. RESULTS

### 3.1. Model selection

First-order terms derived from logistic regression were all significantly negative (all  $p < 0.05$ , Table 1), indicating that functional responses were type II. However, results from AICc revealed that some predator–prey pairs were better fitted by type III or ODE models (Table 1). The logistic regression approach depends on the quality of data at low prey densities. Our experiments ran for 4 d, leading to high consumption at low densities, which mainly rendered negative first-order terms. Therefore, we used the best model with the lowest score from AICc to fit our dataset and derive parameters. The best model for fitting functional response varied with predator size, substrate type, and prey type (Table 1). Most predator–prey pairs of functional responses were most appropriately described by a type II model ( $n = 10$  of 18 models, Table 1). Six functional responses were best described by a type III model, and only 2 were best fitted by using the ODE model. A flexible random model was not the best for any dataset (Table 1).

Table 1. Results of logistic regressions for testing type II or III functional response models and Akaike's information criterion corrected for small sample size (AICc) scores of fitted models. The selected models are in **bold**; ODE: ordinary differential equation

Predator size	Predator–prey system		Logistic regression		AICc score			
	Prey	Substrate	1 <sup>st</sup> term	p	Type II model	Type III model	Flexible model	ODE model
Small	Clam	Simple	−0.049	<0.001	<b>100.984</b>	102.408	103.419	103.418
Small	Clam	Complex	−0.034	<0.001	<b>105.971</b>	112.028	107.311	107.252
Medium	Clam	Simple	−0.032	<0.001	<b>118.036</b>	127.013	120.419	120.377
Medium	Clam	Complex	−0.016	0.009	133.105	<b>119.934</b>	122.088	122.123
Large	Clam	Simple	−0.053	<0.001	<b>114.917</b>	129.855	116.565	116.026
Large	Clam	Complex	−0.040	<0.001	147.081	152.466	146.368	<b>145.319</b>
Small	Scallop	Simple	−0.024	0.003	94.182	<b>92.695</b>	95.129	95.150
Small	Scallop	Complex	−0.017	0.038	89.594	<b>86.142</b>	88.586	88.554
Medium	Scallop	Simple	−0.014	0.011	125.584	<b>118.587</b>	120.030	119.559
Medium	Scallop	Complex	0.062	0.044	108.456	<b>104.002</b>	106.219	106.171
Large	Scallop	Simple	−0.021	<0.001	153.549	128.829	131.260	<b>128.798</b>
Large	Scallop	Complex	−0.018	0.002	137.073	<b>118.264</b>	120.644	119.104
Small	Oyster	Simple	−0.059	<0.001	<b>94.281</b>	96.120	96.253	96.015
Small	Oyster	Complex	−0.054	<0.001	<b>101.373</b>	101.809	103.813	103.812
Medium	Oyster	Simple	−0.047	<0.001	<b>117.279</b>	123.182	119.032	119.025
Medium	Oyster	Complex	−0.048	<0.001	<b>125.215</b>	127.236	127.649	127.651
Large	Oyster	Simple	−0.057	<0.001	<b>134.512</b>	135.454	135.949	135.714
Large	Oyster	Complex	−0.046	<0.001	<b>129.052</b>	137.821	131.105	131.104

### 3.2. Functional responses

Survival of oysters and scallops in controls was 100 %, and only 2 clams died over 4 d (mortality rate: 0.4 %), which indicated that the mortality of prey during the course of experiments can be ignored. Predator–prey pairs, in general, had similar functional responses between simple and complex substrates, because 95 % CIs of bootstrapped parameter estimates overlapped between the 2 substrates for the best model (Fig. 1, Table 1, AICc scores). The functional responses changed from type II to type III with increasing predator size for clams (Fig. 1a–c). For scallops, all functional responses were appropriately described by type III or ODE models (Fig. 1d–f), whereas type II functional responses characterized the interactions between oysters and whelks, regardless of whelk size or habitat complexity (Fig. 1g–i). Only 2 functional responses, medium whelk–clam and large whelk–clam pairs, systematically changed from type II (Fig. 1b,c, red curves; Table 2,  $q = 0$ ) to type III (Fig. 1e,f, blue curves; Table 2,  $q > 0$ ) with increasing complexity of habitat.

For each prey species, the systematic effects of increasing predator size on functional responses were evident, regardless of substrate types. Functional responses drastically increased with increasing predator size regardless of prey type (Fig. 1). For a particular whelk size, the search coefficients for scallops

(0.009–0.035) were significantly lower than for clams (0.021–0.667) and oysters (0.442–0.816) (Table 2). Moreover, there were habitat structure effects nested within this trend, in that the search coefficient was significantly lower in the complex substrate as compared to the simple substrate (Fig. 1, Table 2). However, estimates of handling time did not show a similar trend to search coefficient according to substrate type. Effects of substrate type were not evident, based on the similar handling time between simple and complex substrate (Table 2). Nevertheless, handling times were significantly longer for the small whelks as compared to the medium and large whelks for all 3 prey species in both substrates (Table 2). Furthermore, for a particular whelk size, clams were consumed at a faster rate and oysters took longer to handle regardless of habitat structure (Table 2).

### 3.3. Comparison between estimates and observations of handling time and predator types

To distinguish which factor limits the maximum feeding rate of predatory whelks, we filmed foraging behavior and directly recorded handling time of predators to compare against the estimates derived from the feeding trials. For most predator–prey pairs, the differences between estimates of handling time and empirical observations were  $>0$  (Fig. 2). As there

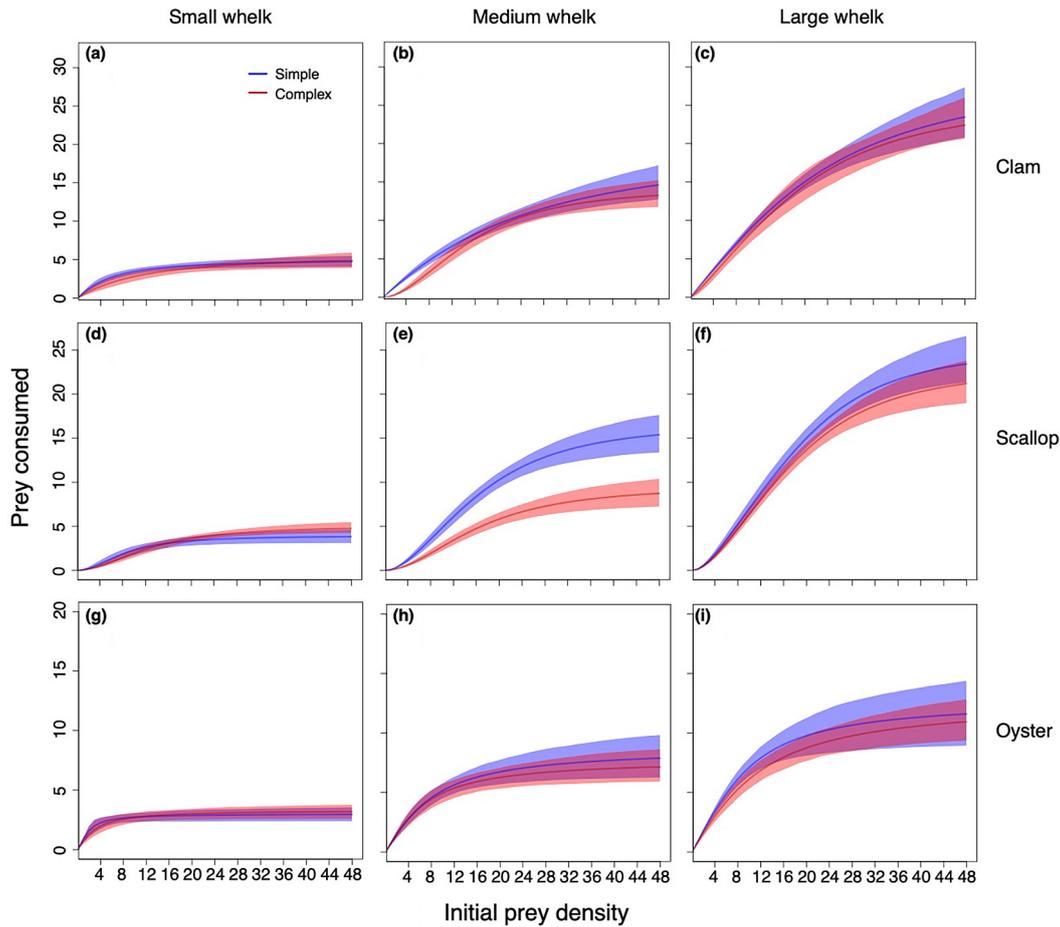


Fig. 1. Functional responses of 3 size classes of the whelk predators *Rapana venosa* towards (a–c) clams *Ruditapes philippinarum*, (d–f) scallops *Chlamys farreri*, and (g–i) oysters *Magallana gigas*. Blue curves are simple habitat structure, red curves are complex habitat structure. Shaded areas are 95% bootstrapped confidence intervals

were no significant differences between estimates and observations of handling time, small whelks were all handling-limited predators when feeding on all 3 prey species, regardless of substrate (Fig. 2a,d,g). Medium whelks, however, were affected by both prey species and substrate (Fig. 2b,e,h). When feeding on clams, medium whelks were digestion-limited irrespective of the habitat complexity (Fig. 2b), but were handling-limited when feeding on oysters (Fig. 2h). However, when feeding on scallops, medium whelks changed from digestion-limited to handling-limited when the habitat complexity increased (Fig. 2e). Large whelks were only limited by handling capacity when dealing with oysters (Fig. 2i).

### 3.4. Scaling relationships and mixed effects model

Predator handling times declined exponentially with increasing predator–prey body mass ratios (Fig. 3), and relationships were qualitatively similar between the 2 habitat structures. This pattern was appropri-

ately described by the global exponential model—Eq. (5) (mean  $\pm$  SE;  $\delta = 0.402 \pm 0.02$   $p < 0.001$  and  $\varepsilon = -2.426 \pm 0.18$ ,  $p < 0.001$ ). Handling-limited predators had longer handling times as compared to digestion-limited predators (Fig. 3).

The results of the linear mixed models indicated that increased predator–prey body mass ratios and predator body mass both drive shorter handling times (Fig. 4a,c, red points). The habitat structure term was not statistically significant in any model, which revealed that habitat complexity did not have an effect on handling times in our cases. Moreover, when the predator changed from digestion-limited to handling-limited, the handling time significantly increased (Fig. 4b, blue point).

## 4. DISCUSSION

In nature, the vast majority of predators are digestion-limited (Weiner 1992), while, in general, handling-limited predators seem to be rare (Jeschke et

Table 2. Estimates of functional response parameters from type II ( $q = 0$ ), type III ( $q = 1$ ), and ordinary differential equation models ( $q = 0.535, 1.616$ ). Parameter  $b$  is the search coefficient or capture rate,  $h$  is the handling time, and  $q$  is the scaling exponent

Predator Size	Prey	Substrate	$b$	SE	p	$h$	SE	p	$q$	SE	p
Small	Clam	Simple	0.324	0.109	0.003	0.772	0.118	<0.001	0		
Small	Clam	Complex	0.159	0.052	0.002	0.678	0.147	<0.001	0		
Medium	Clam	Simple	0.295	0.049	<0.001	0.189	0.032	<0.001	0		
Medium	Clam	Complex	0.021	0.004	<0.001	0.278	0.026	<0.001	1		
Large	Clam	Simple	0.667	0.088	<0.001	0.127	0.014	<0.001	0		
Large	Clam	Complex	0.258	0.107	0.016	0.165	0.020	<0.001	0.535	0.300	0.075
Small	Scallop	Simple	0.015	0.006	0.008	1.017	0.152	<0.001	1		
Small	Scallop	Complex	0.009	0.003	0.003	0.787	0.126	<0.001	1		
Medium	Scallop	Simple	0.023	0.004	<0.001	0.237	0.022	<0.001	1		
Medium	Scallop	Complex	0.011	0.003	<0.001	0.413	0.056	<0.001	1		
Large	Scallop	Simple	0.032	0.024	0.176	0.174	0.012	<0.001	1.616	0.488	<0.001
Large	Scallop	Complex	0.035	0.006	<0.001	0.172	0.012	<0.001	1		
Small	Oyster	Simple	0.816	0.594	0.170	1.324	0.199	<0.001	0		
Small	Oyster	Complex	0.419	0.207	0.044	1.199	0.188	<0.001	0		
Medium	Oyster	Simple	0.442	0.112	<0.001	0.456	0.058	<0.001	0		
Medium	Oyster	Complex	0.472	0.123	<0.001	0.511	0.063	<0.001	0		
Large	Oyster	Simple	0.694	0.140	<0.001	0.311	0.031	<0.001	0		
Large	Oyster	Complex	0.458	0.093	<0.001	0.314	0.038	<0.001	0		

al. 2002). Since the maximum feeding rate (strength of interaction) is determined by whether digestion or handling time is larger (Jeschke et al. 2002), the interactions between handling-limited predators and their prey represent a clear knowledge gap that warrants scrutiny.

To our knowledge, this study presents the first exploration of how functional responses can vary with whether the predator is handling- or digestion-limited, based on environmental context. Our findings indicate that predatory whelks *Rapana venosa* can switch between being handling-limited and digestion-limited, depending systematically on their body mass or the mass ratio to their prey. Habitat complexity, however, only had an effect on handling time for specific predator–prey pairs (i.e. the medium whelk–scallop combination in our study). Moreover, based on the framework where handling time includes the time the predator needs to pursue, ingest, and digest prey (Holling 1959, Jeschke et al. 2002, Brose 2010, Pawar et al. 2012), we propose here that handling-limited predators can be further categorized into 2 types: pursuit-limited (where maximum feeding rate could be influenced by habitat complexity) and ingestion-limited (where maximum feeding rate is affected not by habitat complexity, but by the ingestion capacity of the predator associated with body mass). For instance, in our study, the whelk in the medium whelk–scallop combination is a pursuit-limited predator with a maximum feeding rate that decreases sharply with increasing habitat complexity

(Fig. 1e). One may argue that this reduction arises from the lower search coefficient (parameter  $b$ ) in a complex habitat; however, the search coefficient  $b$  only controls the feeding rate at low prey density (Li et al. 2018, Rosenbaum & Rall 2018), which cannot determine the maximum feeding rate. Examples of ingestion-limited predators are whelks in all whelk–oyster pairs, where maximum feeding rates were not affected by habitat complexity but systematically increased with increasing body mass of predators. Because oysters are sessile organisms with thicker shells and complex morphology, whelks can easily encounter and capture them but need to spend much more time on ingesting (i.e. opening the shell). Put simply, pursuit-limited predators spend more time searching for their prey, while ingestion-limited predators spend more time handling their prey. Even though the maximum feeding rate for both predator types is determined by the sum of the time spent pursuing and ingesting, it is still potentially important to identify the predator type so that one can mechanistically interpret the parameter  $h$  from the functional response model in biologically meaningful terms (Sentis et al. 2013).

The value of these classifications becomes even more apparent in applied ecological contexts, such as the assessment and prediction of the ecological impacts of invasive species. Indeed, the functional response has been widely utilized by invasion ecologists as a means to gauge and forecast the ecological repercussions of non-native species, particularly when

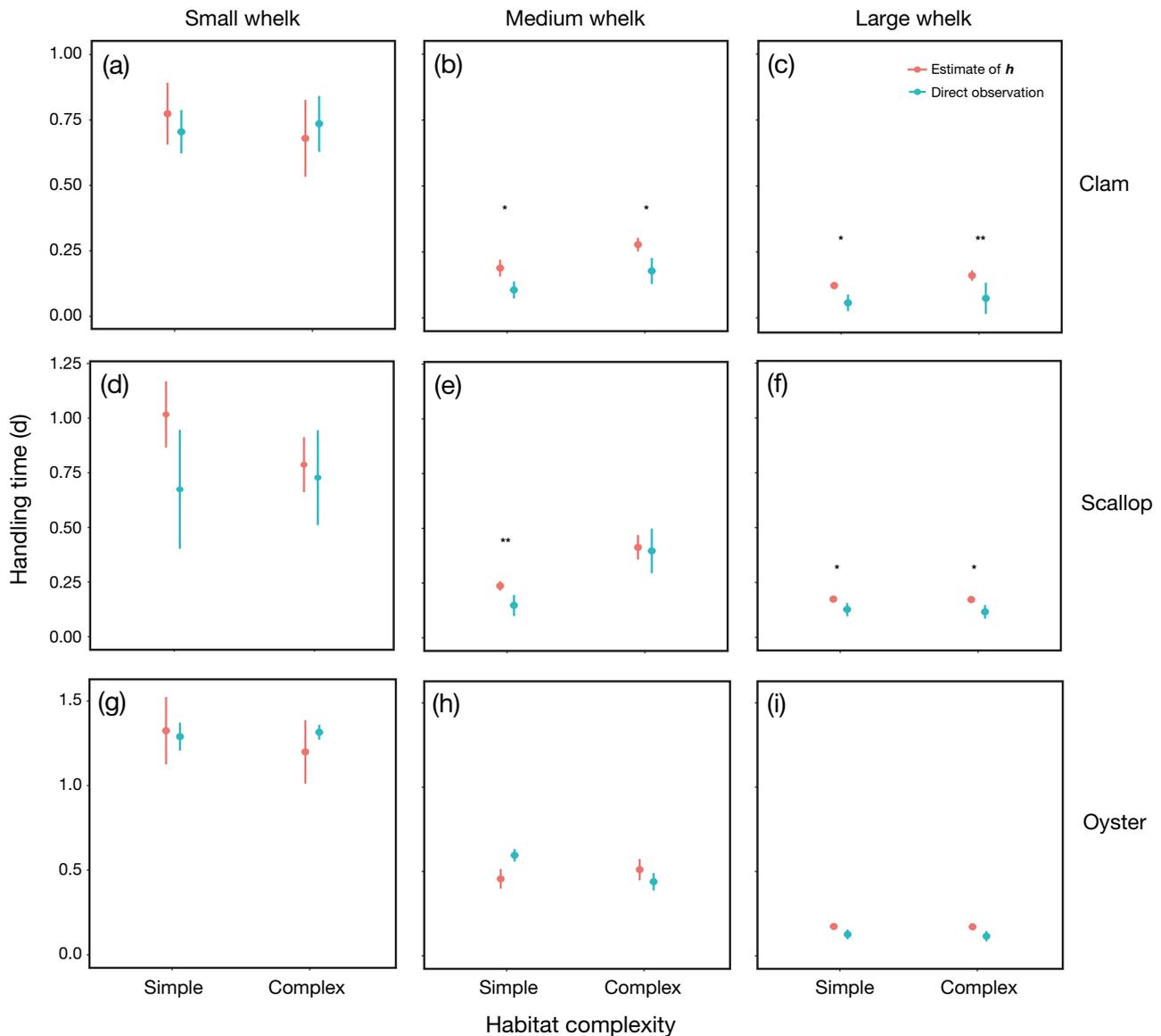


Fig. 2. Estimates of handling time parameter ( $h$ , red) as compared to empirical observations of handling time (blue, mean  $\pm$  SE) for each whelk–bivalve system across 3 predator sizes and 3 prey species in 2 habitat structures. Asterisks denote significant differences between estimates and observations: \* $p < 0.05$ , \*\* $p < 0.01$

juxtaposed with trophically analogous native species (Cuthbert et al. 2019, Mofu et al. 2019). Through our proposed predator classifications, one might potentially predict the impacts of non-native predators in different habitat types with greater precision and nuance. For instance, introducing an ingestion-limited predator into an ecosystem plagued by invasive prey could help regulate the prey population, considering the predator's potentially high consumption rate.

Feeding interactions are specific for each predator–prey system (Jeschke et al. 2002), and thus it would be impractical and unfeasible to resolve every possible pairwise interaction (Barrios-O'Neill et al. 2016). An alternative approach employs body mass-

based models to provide useful generalizations for species-specific interactions (Peters 1983, Yodzis & Innes 1992, Brown et al. 2004, Petchey et al. 2008, Brose 2010, Kalinkat et al. 2013). In the present study, we examined how predator–prey body mass ratios constrain their interaction strength by examining the relationship between body mass ratios and handling time. Handling time generally shows a negative power law with increasing predator mass (Vucic-Pestic et al. 2010, Pawar et al. 2012), but our results here indicate an exponential decline similar to Aljetlawi et al. (2004) and Barrios-O'Neill et al. (2016). We propose that a mechanism underlying this trend is the transition from handling to digestion limitation with increasing predator–prey body mass ratios

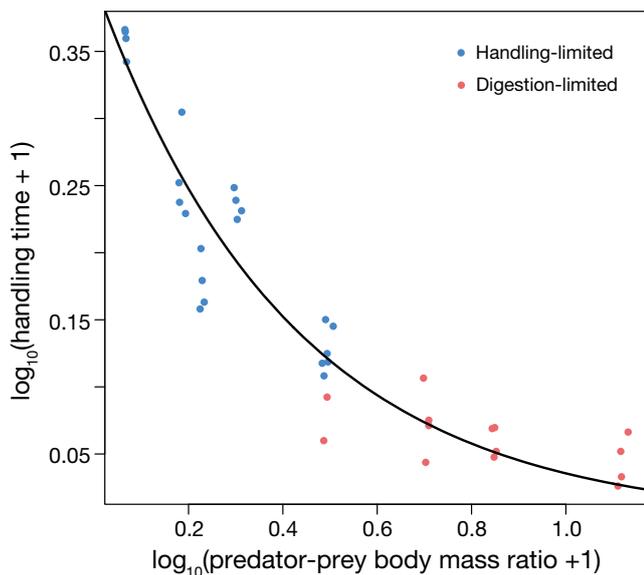


Fig. 3. Scaling of handling times with predator-prey body mass ratios. Handling times follow a global negative exponential relationship;  $\delta = 0.402 \pm 0.02$ ,  $p < 0.001$  and  $\varepsilon = 2.426 \pm 0.18$ ,  $p < 0.001$

(Figs. 3 & 4). Previous studies argued that this trend may also arise from the inconsistencies with metabolic demand at small predator-prey body mass ratios, because small predators are easily impacted by other factors such as interference competition and intraguild predation (Barrios-O'Neill et al. 2014, 2016), leading to a longer handling time.

At the extremes, prey are either too large or too small for predators, meaning that prey are either too difficult or too easy for predators. As a result, predators are either handling-limited or digestion-limited, respectively (Fig. 4). In this way, handling times are not determined by habitat complexity but solely by the predator-prey body mass ratios (Fig. 1c,g). At medium ratios, however, complexity does affect handling time (Fig. 1e). This evidence is consistent with findings of prior studies (Bartholomew et al. 2000, Humphries et al. 2011, Toscano & Griffen 2013, Barrios-O'Neill et al. 2015, 2016). In the present study, habitat complexity only had an effect on the handling time of medium whelk-scallop pair because the complex structure significantly increased the time spent on pursuing prey items. Habitat structure has been long-recognized as a key factor to shape functional responses through the influence of attack rates  $b$  at low prey density, yet our study provides evidence linking systematic increases in habitat complexity to reductions in magnitude of functional response by increasing handling time (Gunn et al. 2021, Froneman & Cuthbert 2022). This was also evident from the behavioral observations of handling

time, which documented that the medium-sized whelks spent much of the time pursuing scallops.

Recent studies have demonstrated that predator type associated with searching (for 2D surface and 3D volume) or encounter strategies (i.e. active mobile, sit-and-wait, filter feeder) are crucial in feeding interactions (Pawar et al. 2012, Barrios-O'Neill et al. 2019). However, the importance of prey types in functional responses has received less attention as compared to predator types (but see Kalinoski & DeLong 2016, Uiterwaal et al. 2017, Uiterwaal & DeLong 2018), particularly for marine generalists. This disparity can be partially explained by the recent surge of functional response literature in the field of invasion ecology. Here, the functional response method is primarily employed as an impact assessment tool to evaluate the potential effects of invasive species (Dick et al. 2014, Dickey et al. 2020). This has further skewed the emphasis towards the study of predator types, as the focus tends to be on non-native predators and their impacts on native ecosystems. We found that prey types had significant effects on parameters of predatory whelk functional responses (Table 2), similar to studies on beetles and damselflies (Uiterwaal et al. 2017, Uiterwaal & DeLong 2018).

Vermeij (1987) argued that marine bivalves generally utilize 2 major modes of antipredator defense: avoidance or armor. In our study, scallops mainly used the former strategy to reduce encounter rates via actively jumping to avoid their predators, while oysters relied upon their shell morphology and thickness to reduce the handling efficiency of their predators. In comparison, clams are at the midpoint of the armor-avoidance spectrum, as they may utilize both defensive strategies (Seitz et al. 2001). Our findings revealed that avoidance-prey may mainly rely on habitat structure as protection. The search coefficient in complex habitats was significantly lower than simple habitats for the whelk-scallop system, thereby leading to lower maximum feeding rates (Fig. 1d-f). However, our results revealed a new framework that if the predator was large enough with a great enough searching ability, the refuge may lose its effect (i.e. large whelk-scallop system).

Seitz et al. (2001) suggested that armored prey highly depend upon morphological defenses and relative body size to reduce predator handling efficiency. Our findings regarding oysters strongly support this suggestion. In this predator-prey system, maximum feeding rates were not affected by the habitat structure, yet they did increase with increasing predator size (Fig. 1g-i). The intermediate spe-

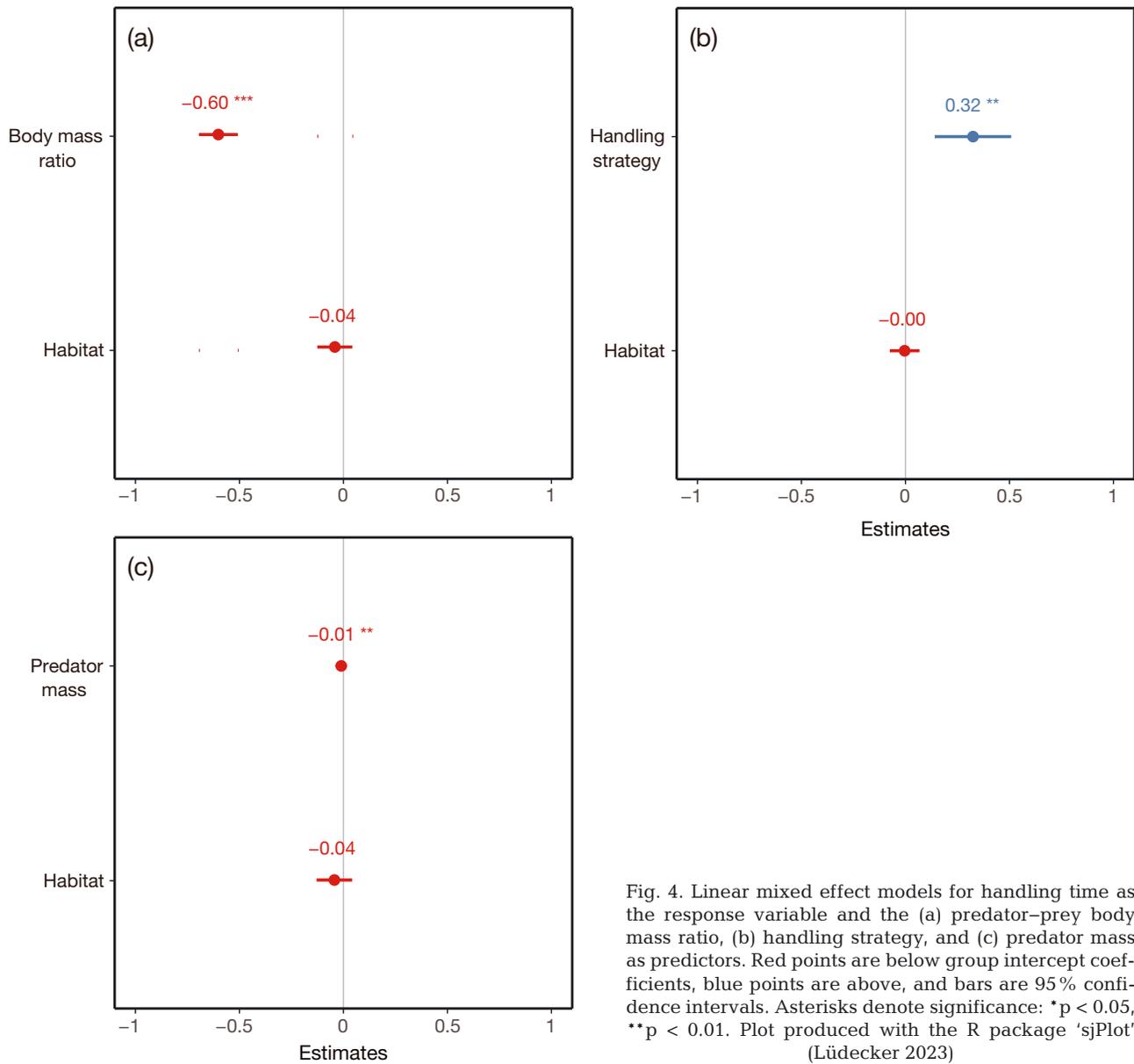


Fig. 4. Linear mixed effect models for handling time as the response variable and the (a) predator-prey body mass ratio, (b) handling strategy, and (c) predator mass as predictors. Red points are below group intercept coefficients, blue points are above, and bars are 95% confidence intervals. Asterisks denote significance: \* $p < 0.05$ , \*\* $p < 0.01$ . Plot produced with the R package 'sjPlot' (Lüdecker 2023)

cies in our study appeared to have used the armor strategy to defend against the whelk, because the complex habitat did not affect the maximum feeding rate. One reason is that whelks can burrow into sand to dig out clams, which made the avoidance behavior (burrowing) unviable. Thus, we argue that prey defense strategies could usefully refine estimates of feeding interactions in complex food webs across biomes and habitats.

While the use of 3 different prey species provides a broad range of body sizes and avoidance strategies, which adds a level of ecological realism to our study, certain inherent limitations in our experimental design need to be acknowledged. The primary chal-

lenge stems from the simultaneous variation in body sizes and predator-avoidance strategies across the 3 different prey species used in the study. This multiplicity of variables impedes the ability to isolate the effects of predator-prey body mass ratios. Consequently, observed differences in functional responses may not solely be attributed to variations in body mass ratios, but could also be influenced by species-specific traits and defensive strategies of the prey. Moreover, the shift in foraging limitations observed in predatory whelks as they increase in size presents another layer of complexity. This raises the question of whether the change in functional responses is driven predominantly by the alteration in hunting

strategies or the size of the predator itself. Fig. 3 shows a strong correlation between biomass ratio and types of limitation, illustrating the intertwined nature of these variables. Although the decrease in handling time was attributed to a transition in prey-handling strategies, this conclusion could be confounded by the predator–prey body mass ratio. Future studies should strive to further isolate these factors, to enhance the resolution in our understanding of predator–prey interactions. In spite of these limitations, we feel confident in proposing that when using functional responses to describe feeding interactions, there is further utility in explicitly considering prey defense strategy, in addition to body mass and habitat structure.

*Data and code availability.* The data and R code supporting our findings in this study are available from the Dryad Data Repository at <https://doi.org/10.5061/dryad.x69p8czns>.

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## Appendix. Additional data

Table A1. Results of bootstrapping analyses (n = 100) for Akaike's information criterion scores corrected for small sample size (AICc) and confidence intervals [CIs] of fitted models. The selected models are in **bold**; ODE: ordinary differential equation

— Predator-prey system —			— AICc scores and CIs —			
Predator size	Prey	Substrate	Type II model	Type III model	Flexible model	ODE model
Small	Clam	Simple	<b>100.09 [99.55, 100.62]</b>	101.19 [100.68, 101.69]	101.64 [101.09, 102.19]	102.04 [101.46, 102.63]
Small	Clam	Complex	<b>104.31 [103.45, 105.16]</b>	109.74 [108.63, 110.85]	105.51 [104.72, 106.30]	105.12 [104.05, 106.19]
Medium	Clam	Simple	<b>117.53 [114.65, 120.42]</b>	124.83 [122.09, 127.57]	118.95 [116.44, 121.45]	118.88 [116.81, 120.94]
Medium	Clam	Complex	132.77 [131.63, 133.93]	119.34 [118.08, 120.61]	120.35 [118.91, 121.78]	120.29 [118.72, 121.86]
Large	Clam	Simple	<b>113.02 [111.43, 114.62]</b>	127.95 [126.48, 129.42]	114.13 [112.66, 115.59]	115.29 [114.11, 116.49]
Large	Clam	Complex	148.37 [144.77, 151.97]	150.76 [146.37, 155.14]	144.61 [140.86, 148.37]	<b>143.66 [139.38, 147.29]</b>
Small	Scallop	Simple	93.18 [92.58, 93.79]	<b>91.45 [90.68, 92.22]</b>	93.10 [92.28, 93.92]	92.92 [92.14, 93.69]
Small	Scallop	Complex	88.57 [86.81, 90.34]	<b>83.53 [80.56, 86.50]</b>	85.44 [82.28, 88.59]	85.23 [82.07, 88.78]
Medium	Scallop	Simple	124.91 [121.87, 127.93]	<b>116.93 [112.97, 120.89]</b>	118.39 [114.86, 121.92]	117.98 [114.55, 121.42]
Medium	Scallop	Complex	107.40 [106.52, 108.28]	<b>102.26 [101.43, 103.09]</b>	104.01 [103.19, 104.82]	104.94 [104.05, 105.94]
Large	Scallop	Simple	154.52 [148.02, 161.02]	129.89 [126.15, 133.63]	132.01 [128.22, 135.81]	<b>127.07 [125.84, 128.31]</b>
Large	Scallop	Complex	137.47 [133.60, 141.33]	<b>117.15 [114.80, 119.49]</b>	119.32 [116.85, 121.79]	117.89 [115.96, 119.82]
Small	Oyster	Simple	<b>92.59 [91.97, 93.21]</b>	95.42 [94.93, 95.91]	94.55 [93.99, 95.12]	95.04 [94.43, 95.41]
Small	Oyster	Complex	<b>99.76 [99.06, 100.46]</b>	100.47 [99.91, 101.03]	101.52 [100.83, 102.21]	101.08 [100.44, 101.72]
Medium	Oyster	Simple	<b>115.84 [114.59, 117.09]</b>	121.41 [119.80, 123.03]	116.92 [115.71, 118.13]	115.86 [114.73, 116.99]
Medium	Oyster	Complex	<b>123.74 [122.52, 124.97]</b>	124.97 [123.69, 126.25]	124.45 [123.29, 125.61]	124.09 [122.94, 125.25]
Large	Oyster	Simple	<b>130.43 [128.15, 132.72]</b>	141.33 [138.96, 143.71]	131.02 [128.62, 133.41]	132.39 [129.81, 134.98]
Large	Oyster	Complex	<b>126.53 [125.01, 128.04]</b>	135.10 [132.93, 137.27]	127.47 [126.12, 128.81]	127.06 [125.76, 128.37]

Table A2. Student's *t*-test between estimates and observation of handling time for all predator-prey pairs. Significant effects are in **bold**

Predator size	Prey	Substrate	<i>t</i>	df	p
Small	Clam	Simple	0.829	5	0.444
Small	Clam	Complex	-0.451	5	0.671
Medium	Clam	Simple	2.621	5	<b>0.047</b>
Medium	Clam	Complex	2.807	5	<b>0.038</b>
Large	Clam	Simple	3.092	5	<b>0.027</b>
Large	Clam	Complex	5.582	5	<b>0.003</b>
Small	Scallop	Simple	1.844	5	0.125
Small	Scallop	Complex	0.209	5	0.842
Medium	Scallop	Simple	5.542	5	<b>0.003</b>
Medium	Scallop	Complex	0.236	5	0.823
Large	Scallop	Simple	2.812	5	<b>0.037</b>
Large	Scallop	Complex	2.731	5	<b>0.041</b>
Small	Oyster	Simple	0.356	5	0.736
Small	Oyster	Complex	-1.846	5	0.124
Medium	Oyster	Simple	-4.264	5	<b>0.008</b>
Medium	Oyster	Complex	1.199	5	0.284
Large	Oyster	Simple	2.147	5	0.085
Large	Oyster	Complex	-1.074	5	0.332

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