

Hierarchical models to predict predation in complex trophic communities

Benjamin Mercier^{1,2,‡} Arthur Andrew Meahan MacDonald^{1,2} Dominique Gravel^{1,2}

¹ Université de Sherbrooke ² Québec Centre for Biodiversity Sciences

[‡] Equal contributions

Correspondance to:

Benjamin Mercier — benjamin.b.mercier@usherbrooke.ca

Trophic interactions make the backbone of ecological communities. From herbivory to predation, these interactions of varying strength shape ecosystem and their related functions. There is a pressing need to be able to predict interaction strength at the scale of whole communities. While functional responses focus at the pairwise interaction level, we question here if the same underlying mechanisms could be leveraged to make predictions at the scale of the community. In this study, we develop 4 hierarchical models of increasing complexity based on the type I and the type II functional responses to predict biomass fluxes between consumers and resources at the community level. The main objective is to determine if simple mechanism such as mass action (type I) and the saturation of fluxes (type II) are sufficient to predict biomass fluxes. To do so, we collected 19 Ecopath networks encompassing 1380 interactions across marine, aquatic and terrestrial ecosystems. While we can not reject the mechanism of saturating fluxes (type II), our results suggest that a mass action mechanism is sufficient and more robust, in the context of our data, to predict biomass fluxes between consumers and resources at the community level. We also recovered the expected allometric relationships between consumers body mass and their space clearance rate parameters within the mass action model, further solidifying our findings. Further modelisation is needed, specifically a trait-matching model with more data, to develop a model generalizable to more taxons and types of trophic interactions.

1 Trophic interactions make the backbone of ecological communities (Bellingeri & Bodini 2016; DeLong 2021;
2 Wootton & Emmerson 2005), linking every component through nutrient and energy flows (Lindeman 1942).
3 Consumer-resource interactions of varying strength play a crucial role in shaping important ecosystem functions
4 and processes (Curtsdotter *et al.* 2019; Duffy 2002; Koltz *et al.* 2018; Montoya *et al.* 2003; Wilmers *et al.*
5 2012) such as disease dynamics, invasive species and biogeochemical cycles (Estes *et al.* 2011). Identifying
6 species interactions and quantifying their strength is necessary to understand community composition (Paine
7 1992), stability (Bascompte *et al.* 2005; de Ruiter *et al.* 1995; Neutel 2002; Nilsson & McCann 2016) and the
8 resulting associated ecosystem services (Montoya *et al.* 2003). Global changes have a diversity of impacts on
9 species themselves, but also how they interact and the resulting assemblages and functioning (Koltz *et al.* 2018;
10 Lurgi *et al.* 2012). Empirical observation of these interactions and the evaluation of their strength is however
11 challenging, if not unfeasable due to their sheer amount, sampling biases and the emergence of novel
12 interactions between species that never co-occurred (Aguiar *et al.* 2019; Jordano 2016; Wootton & Emmerson
13 2005). The study of ecological networks has therefore recently moved to the development of predictive tools to
14 overcome the limitations associated with empirical sampling of trophic interactions (Poisot *et al.* 2016).
15 Different models are derived from food web theory, such as the niche model (Williams & Martinez 2000), the
16 nested-hierarchy model (Cattin *et al.* 2004), trait-matching model (Bartomeus *et al.* 2016) or physical
17 constraints (Portalier *et al.* 2019). More recently, Strydom *et al.* (2021) developed a general framework to
18 predict interaction probabilities between species in a community context. These methods are however mostly
19 qualitative, i.e. they are meant to predict if there is an interaction or not, and there is a pressing need to expand
20 them to quantitative interactions, where the strength of interaction between any two organisms is described.
21 There are many definitions of interaction strength (Berlow *et al.* 2004), and among them biomass flows can be
22 particularly suited for the development of predictive models. Biomass flows between consumers and resources
23 can be derived from functional traits, with the promise of a standardized measure independent of taxa involved
24 (Berlow *et al.* 2004). Quantitative predictive models of biomass flows might also offer potential support to the
25 study of biodiversity and ecosystem functioning relationship, as it seeks to depict all energy flows within
26 communities (Barnes *et al.* 2018). Biomass flows are defined as a quantity of resource biomass that is
27 consumed by a consumer per unit area and unit of time, reporting how energy circulates through the food web
28 (Lindeman 1942). Interaction strengths between consumers and resources is closely related to predation rate in
29 a food web model, namely the functional responses (Rall *et al.* 2012). Functional response theory aims at
30 describing the change in feeding rate of a consumer, or how many prey or resource a consumer can predate per

31 unit area over time, relative to prey or resource availability (Holling 1959a, b; Solomon 1949). Where the
32 functional response describes the actual number of individual prey or resource predated by a consumer per unit
33 area over time, biomass flows describes the amount of biomass flowing from a prey or resource to a consumer
34 per unit area over time. Since both quantities report the rate of the same underlying process that is predation, we
35 anchored the development of our modeling approach in functional response theory.

36 A fundamental principle underlying the majority of functional responses is the mass action, stating that predator
37 and prey move randomly in an area and encounter at a rate proportional to the product of their abundance and
38 their velocity. Here we will focus on the two most commonly used types of functional responses. The type I
39 functional response describes mass action only, where the amount of resource consumed depends on the
40 resource and consumer densities, and the rate (formerly referred to as attack rate and hereafter space clearance
41 rate (DeLong 2021)) at which a consumer searches its home range for resources, leading to random encounters
42 followed by detection, attack and consumption. The type II functional response describes the same process as
43 the type I, but with the addition that consumption saturates with prey availability because of the time required to
44 process prey. These processes are influenced by a multitude of functional traits and environmental conditions
45 (Beardsell *et al.* 2021, 2022). The space clearance rate parameter varies with consumers and resources intrinsic
46 characteristics such as absolute and relative velocities, perception of the environment and cognitive abilities
47 (DeLong 2021). It is also influenced by externalities such as habitat complexity (Barrios-O'Neill *et al.* 2016;
48 Hall *et al.* 2000; Manatunge *et al.* 2000) and the presence of refugia (Hoddle 2003) impeding detection
49 probability. The dimensionality of an interaction, whether it takes place in a two or three dimensional plane,
50 also impacts encounter rates and detection probability (Pawar *et al.* 2012, 2019). For instance, a predatory bird
51 searching for preys from above or fishes grazing the benthic surface are examples of 2D planes while aerial
52 insectivorous birds pursuing flying insects or fishes chasing preys in the water column would be in a 3D plane.
53 Functional response theory therefore makes a good start to develop predictive models of quantitative
54 interactions since widely measured functional traits can be combined with consumer and prey density to predict
55 biomass flows.

56 The space clearance rate, in units of space per time, reports the amount of area search by the predator in a time
57 interval. As with many biological processes, the space clearance rate was shown to vary with consumers body
58 mass. Indeed, multiple studies, summarized in the FoRAGE database (Uiterwaal *et al.* 2022), showed an
59 allometric scaling between the space clearance rate and the body mass of consumers. This observation is
60 coherent with (Hirt *et al.* 2017, 2020) who documented that the maximum velocity of an organism scales with

61 its body mass. Handling time is also expected to follow the same scaling relationship (DeLong 2021), although
62 recent studies are now suggesting that consumers handling time would not be as important at natural resources
63 densities (Beardsell *et al.* 2021; Chan *et al.* 2017; Coblenz *et al.* 2023; Preston *et al.* 2018). Ultimately, an
64 accurate evaluation of these parameters is necessary as they are widely used in theoretical models (Brose *et al.*
65 2006; Brose *et al.* 2008; Pawar *et al.* 2012). Restraining the parameter space could greatly bonify studies of
66 species coexistence, community stability and trophic regulation. It could also help the parameterization of
67 global ecosystem models used for biodiversity scenarios (Harfoot *et al.* 2014}). Following (Yodzis & Innes
68 1992), there are a few meta-analyses looking at the scaling of feeding rates with body-mass (Rall *et al.* 2012).
69 These are however concentrated on a re-analysis of univariate functional responses, mostly from experimental
70 studies, and there is currently no study aiming at reconstructing quantitative interaction networks.

71 Our main objective is to test if we could model quantitative interactions in complex food webs with easily
72 accessible information such as abundance and body mass. We compared statistical models derived from
73 functional response theory, including type I and type II forms. We also investigate if allometric relationships
74 between space clearance rate, handling time and consumer body mass can contribute to the prediction of
75 biomass flows in diverse food webs. To do so, we developed four hierarchical models of pairwise quantitative
76 interactions of increasing complexity and evaluated them with empirical data of biomass flows between
77 consumers and resources. We curated Ecopath networks (Christensen *et al.* 2005) describing marine, aquatic
78 and terrestrial food webs and extracted 1380 pairwise trophic interactions between consumers and resources.
79 Each model represents its own hypothesis and their comparison allow the evaluation of different mechanisms
80 driving interactions.

81 Material and methods

82 A litterature search was performed to gather empirically sampled trophic networks with measurements of
83 biomass flows from resources to consumers, along with population densities. Food web data are notoriously
84 heterogeneous (Mestre *et al.* 2022) and we therefore relied on Ecopath models (Christensen *et al.* 2005) to
85 normalize data collection. Ecopath is a modelling software that relies on a mass-balance premiss and a
86 multitude of parameters (production/biomass ratio, consumption/biomass ratio, diet compositions etc.) to
87 provide a realistic static image of the flows of biomass between resources and consumers in an ecosystem
88 (Christensen *et al.* 2005). It was shown the Ecopath methodology reduces biases in comparative analyses

89 among food webs (Brimacombe, in review). We therefore collected openly available models from Ecobase
90 (Colléter *et al.* 2013) and worked with a subset of the models present in (Jacquet *et al.* 2016). Taxonomic
91 resolution of Ecopath models is highly variable and it is not uncommon that species are lumped into functional
92 groups. The models were therefore selected based on the taxonomic resolution with the criteria that most nodes
93 must be resolved at the species level, or that species within functional groups were taxonomically resolved. We
94 thus curated 19 Ecopath models (detailed list in supplementary material) from aquatic, marine and terrestrial
95 environments (fig. 1), and trophic guilds spanning from mammal carnivores and herbivores, birds, pelagic
96 carnivorous and herbivorous fish, demersal carnivorous and herbivorous fish and invertebrates.

97 [Figure 1 about here.]

98 Species identity in the Ecopath models were validated with the original publication and estimates of adult mean
99 body mass was retrieved from literature. Body mass for terrestrial species came from different sources such as
100 the GATEWAv database (Brose 2018), the original publication for which the Ecopath model was developed or
101 grey literature. Body mass for marine and freshwater species came from Fishbase (Froese *et al.* 2023) and
102 Sealifebase (Palomares *et al.* 2023). When only body length was available, Fishbase and Sealifebase calculated
103 weight from body length using a bayesian length-weight model. The midpoint between the minimum and
104 maximum measurements was taken when a mean was not available. Density N (number of individuals per unit
105 surface, N/km^2) was computed by dividing total biomass per unit surface B (metric tons/ km^2) by mean body
106 mass M (metric tons). The 19 Ecopath models were aggregated in an edge list with quantitative biomass flows
107 (metric tons/ km^2/year), for a total of 1380 interactions between 154 consumer species and 153 resource
108 species.

109 Model description

110 We developed four different hierarchical models of increasing complexity based on the type I and type II
111 functional responses, and a null model. Models were then parametrized with Hamiltonian Monte Carlo
112 (Monnahan *et al.* 2017), compared and ranked from better to worst based on their prediction accuracy. The
113 functional form of these relationships are presented below.

114 **Model 0 - Null model**

115 The null model acts as a basis of comparison with the other models and does not portray any ecological realism
116 of a trophic interaction. Model 0 hypothesizes that the flow of biomass F_{ij} from a prey i to its predator j is
117 constant with average K , irrespective of predator identity:

$$F_{ij} = K$$

118 **Model 1 - General mass action**

119 Model 1 implements a general version of the type I functional response and thereby focuses on the law of mass
120 action. The flow of biomass F_{ij} depends on the available prey biomass B_i and the abundance of the predator N_j
121 where they encounter each other at a given the α space clearance rate of the consumer N_j . Explicitely, only the
122 consumer's mobility is considered as it searches for resources. For the purpose of comparison, model 1
123 hypothesizes that all consumers have the same space clearance rate α :

$$F_{ij} = \alpha B_i N_j$$

124 **Model 2 - Consumer-specific mass action**

125 Model 2 follows the previous one with the hypothesis that space clearance parameter α_j is a specific parameter
126 for each consumer species j :

$$F_{ij} = \alpha_j B_i N_j$$

127 **Model 3 - Single-species saturating model**

128 Model 3 keeps the assumptions of model 2 with the addition of handling time, thereby representing a single
129 species Type II functional response. The space clearance rate parameter α_j and the handling time h_j are both
130 consumer-specific:

$$F_{ij} = \frac{\alpha_j B_i N_j}{1 + h_j \alpha_j B_i N_j}$$

131 **Model 4 - Multi-species saturating model**

132 Building on model 3, model 4 implements a multi-species version of Type II functional response (Smout *et al.*
 133 2010). Parameters are the same as the ones used in model 3, the difference is found at the denominator where
 134 handling is aggregated over all species in the food web:

$$F_{ij} = \frac{\alpha_j B_i N_j}{1 + h_j \alpha_j \sum_{i=1}^{n_{prey}} B_i N_j}$$

Model name	Model equation	Number of parameters
Null model	$F_{ij} = K$	2
General mass action	$F_{ij} = \alpha B_i N_j$	2
Predator specific mass action	$F_{ij} = \alpha_j B_i N_j$	157
Single species saturating model	$F_{ij} = \frac{\alpha_j B_i N_j}{1 + h_j \alpha_j B_i N_j}$	313
Multi species saturating model	$F_{ij} = \frac{\alpha_j B_i N_j}{1 + h_j \alpha_j \sum_{i=1}^{n_{prey}} B_i N_j}$	313

135 F_{ij} represents the flux of biomass (metric tons/km²/year), K is a parameter representing mean biomass flow
 136 (metric tons/km²/year), α is the general space clearance rate (km²/consumer/year), α_j is the
 137 consumer-specific space clearance rate (km²/consumer/year), B_i is the prey biomass (metric tons/km²), N_j is
 138 the consumer abundance (individual/km²) and h_j is the consumer handling time
 139 (metric tons of resource biomass/km²/year).{#tbl:table_model}

140 **Model evaluation**

141 All biomass fluxes and body-mass were log-transformed. Biomass fluxes were modelled with a hierarchical
142 bayesian approach where F_{ij} follows, after being log-transformed, a normal distribution with mean μ and
143 standard deviation σ , where the mean corresponds to the five different models described above respectively.
144 Species-specific parameters α_j and h_j were considered as random effects following normal distributions. As we
145 lacked prior knowledge on potentiel distribution for the parameters, we opted for generic weakly informative
146 priors. The mean and standard deviation for α and h_j were 0 and 1 respectively and were the same for all
147 models. The analysis was performed with Stan version 2.32.2 (Stan Development Team 2024) via the package
148 rstan in R version 4.3.3 (R Core Team 2024).

149 After fitting the data to each model respectively, we used the LOO package (Vehtari *et al.* 2024) to compute the
150 expected log pointwise predictive density (ELPD) to perform a leave-one-out (LOO) cross validation based on
151 (Vehtari *et al.* 2017) to estimate prediction accuracy. We computed Pareto diagnostic values per model to
152 evaluate reliability. Models were ranked by predictive accuracy based on their respective ELPD score. We also
153 compared the ELPD score between models to evaluate prediction accuracy and their bayesian R^2 (Gelman *et al.*
154 2019). Finally, we tested with linear regression allometric relationships of the space clearance rate parameter α
155 and handling time h_j with consumer body mass.

156 **Code and data availability**

157 All the R scripts for model evaluation and figures are available on Github at
158 <https://github.com/BenMerSci/master>.

159 **Results**

160 All models (with the exception of the null hypothesis) had good fit to the data, with R^2 ranging from 0.697
161 (model 1 - details at tbl. ?? and R^2 posterior distributions in Appendix 2) to 0.835 (model 3). The model
162 ranking based on the predictive accuracy with LOO, where higher values are better, revealed that the best
163 performing model is the single species saturating model (model 3) with an ELPD score of -2452.8, almost equal
164 to the multi species saturating model (model 4) and the consumer specific mass action model (model 2) with
165 ELPD scores of -2713.5 and -2749.4 respectively. The the null model (model 0) and the general mass action

model (model 1) followed with ELPD score of -3529.1 and -4056.1, respectively. Model ranking reveals that, with the exception of model 4, every hypothesis that is added to the model contribute significantly to ELPD and R^2 . The most significant increases is observed between model 1 and model 2, indicating that, once we account for mass action (model 1), the most important element is predator specific consumption rate (model 2). Adding saturation only marginaly improves the fit (model 3), while accounting for multi-species saturation has no significant impact (model 4).

It is to be noted that both model 3 and model 4 had higher Pareto K diagnostic values (> 0.7), which might indicate non-robust model or highly influential observations (Vehtari *et al.* 2017).

Model predictive density (ELPD)	Expected log pointwise difference	Standard error	Effective number of parameters (p-LOO)	Number of parameters	mean R^2
model 3 -2455.4	0.0	0.0	202.5	313	0.833
model 4 -2717.7	-	28.8	149.5	313	0.795
model 2 -2751.3	-	30.2	142.2	157	0.803
model 0 -3529.1	-	35.7	2.4	2	0.000
model 1 -4056.5	-	37.3	2.1	2	0.696
	1073.7	1601.1			

Model ranking based on ELPD with LOO. Models are ranked from best to worst based on their predictive accuracy with the LOO package.{#tbl:table_ranking}

Model comparison suggests that mass action only catches most of the variability in biomass fluxes, but the graphical representation of predicted biomass flows against observed biomass flows reveals a very significant bias that is solved with species-specific space clearance rates (figure fig. 2). Since the bias in predictions disappears in all three species-specific models and that model 1 ranked below our null model, it was dismissed. Model ranking and the R^2 suggest the single species saturating model (model 3) is better than model 2 and 4, but the difference is hardly significant both from statistics (Table tbl. ??) and graphical representation (figure fig. 2). The consumer specific mass action model (model 2) and the multi-species saturating model (model 4)

183 are the closest together regarding their ELPD score. Furthermore, the added multi-species aspect of model 4,
184 relative to the single-species model 3, does not improve the fit, neither from statistics nor from graphical
185 representation, therefore dismissing model 4. The *extreme* Pareto K values of model 3 and 4 would also suggest
186 that both models might not be suited to make prediction as is (Vehtari *et al.* 2017).

187 [Figure 2 about here.]

188 At first glance based on the model ranking and the R^2 , the single species saturating model (model 3) seems to
189 have better prediction accuracy than model 2 and 4. The prediction against observations plots is hinting at the
190 same conclusion, where all three models look pretty similar but the points in model 3 are more grouped around
191 the diagonal line. The consumer specific mass action model (model 2) and the multi-species saturating model
192 (model 4) are the closest together regarding their ELPD score. Since model 3 and model 4 are both based on the
193 type II functional response, showing barely no difference in fit and model 3 ranking better, we dismissed model
194 4. This decision is also based on parsimony, the extreme Pareto K values and model 2 having a higher R^2 than
195 model 4. Posterior distributions of the space clearance rate (figure fig. 3) are very similar across the three
196 models, with the distinction that the distribution of model 3 and 4 were wider while model 2 were narrower.
197 Handling time also varies significantly between species (figure fig. 4), with some species having very wide
198 distributions and without clear differences between trophic guilds.

199 [Figure 3 about here.]

200 [Figure 4 about here.]

201 We lastly investigated the relationships between space clearance rate, handling time and body mass. We found a
202 significant relationship between body masses and the space clearance rate for the specific mass action model
203 (model 2, figure {fig. 5}.A). Relationship with the space clearance rate and consumers body mass was
204 significant with a slope of 0.98 (p-value < 0.05, adjusted R^2 of 0.56). This relationship was not significant
205 however for space clearance rates extracted from model 3 (model 3, figure fig. 5 .B and fig. 5 .C), neither was
206 the relationship between body mass and handling time.

207 [Figure 5 about here.]

208 **Discussion**

209 The motivation of this study was to develop predictive models of quantitative interactions for entire food webs.
210 There are already several techniques to predict the occurrence of interactions and to reconstruct binary
211 interaction networks such as the niche model (Williams & Martinez 2000), trait-matching model (Bartomeus *et*
212 *al.* 2016) and machine learning models (Pichler *et al.* 2020). There are also quite a few meta-analyses of
213 functional responses, none of them can be applied to entire food webs as they were mostly based on single
214 species analyses. Here we developed these one step further with the prediction of biomass flows as a function of
215 mass action, allometric scaling and the full web composition. To do so, we investigated an ensemble of models
216 to predict biomass flows between populations of consumers and resources inspired from functional response
217 theory. Four mechanistic model of increasing complexity based on the type I and the type II functional response
218 were compared to test different hypotheses. In contrast with functional response studies, where the variation of
219 consumption rates of consumers with resource density is evaluated, here we attempted to predict biomass fluxes
220 between all pair of species within a community context. Upon initial inspection of the fits of each model, it
221 appears that models based upon functional response type I (mass action model) and type II (saturating model)
222 are well suited to predict biomass fluxes. We discuss hereafter the inherent properties of each model and
223 compare them regarding their predictive capabilities of biomass fluxes. Specifically, we compared the different
224 underlying mechanisms and discuss whether mass action is enough or if the incorporation of saturation with
225 consumers handling time is an important addition to predict biomass flows. We follow by exploring whether the
226 expected allometric relationships with both parameters of interest (space clearance rate and handling time) are
227 observed. We conclude by addressing the limitations of the study and potential next avenues for improving the
228 model.

229 Overall, based on the Bayesian R², the model ranking (table *tbl. ??*) and their graphical representation, we found
230 that all the models (except the null model) had a good fit. While model 1 looks like a good one by looking at the
231 performance metrics, it had a discernable and clear bias in terms of data fitting which undoubtedly arose from
232 the non-specific space clearance rate. Model 1 portrayed a mass action process where consumption rates simply
233 follows encounters between consumers searching their environment for resources based on a rate at which they
234 clear space (DeLong 2021; O'Dwyer 2019). Space clearance rate is expected to vary with species body mass
235 and other traits (DeLong 2021; Rall *et al.* 2012) and our data comprised a variety of organisms ranging from
236 small fish to terrestrial mammals. The improvement in fit of model 2 in contrast to model 1 further consolidate

237 this hypothesis, where the implementation of a consumer-specific space clearance rate greatly improved model
238 fitting and resulting R^2 , thus dismissing model 1. With this said, model 2, 3 and 4 all had similar outcomes
239 regarding R^2 and predictive accuracy (table [tbl. ??](#)), while portraying different ecological mechanisms. While
240 model 2 implemented a mass action process with consumer-specific space clearance rates, model 3 and 4
241 incorporated a second mechanism of saturating biomass fluxes with consumers handling time. Both models 3
242 and 4 were based upon a type II functional response, where the main difference was that model 3 was saturating
243 biomass fluxes over the biomass of one prey (single-species) while model 4 was accounting for the biomass of
244 all prey species available in the community (multi-species). While we expect consumers consumption rates over
245 a resource to vary depending on the availability of all its resources of interest (Smout *et al.* 2010), the
246 multi-species saturating model underperformed compared to the single-species saturating model. Accounting
247 for all resource biomass did not seem to improve the fit, thus dismissing model 4. Given the great diffrence in
248 number of parameters between model 2 and 3 (table ([table:table_model?](#))), their similar fit, and the high
249 Pareto K values of model 3, model 2 seems to be the most parcimonious choice. Additionally, there seems to be
250 a tradeoff between the space clearance rate and handling time parameter which introduces variability in the
251 estimation of space clearance rate (figure [fig. 3](#)). This tradeoff also seems to impact the expected allometric
252 relationships of space clearance rate and handling time with consumers body mass in model 3 (figure [fig. 5](#)
253 -B-C). Even though model 3 had the highest R^2 and ELPD score, it may also suffer from misspecification as
254 indicated by the high Pareto K values (Vehtari *et al.* 2017). While the saturating model might still be relevent
255 and can not totally be dismissed from our analysis, it seems that a simple model such as our consumer-specific
256 mass action model gives a satisfying approximation of biomass fluxes.

257 Allometric relationships

258 The form of the functional response has been the subject of a longstanding debate (Barbier *et al.* 2021) since
259 first formalized by Holling (1959a). The statistical models we developed operate on a different scale than single
260 species functional response studies, taking advantage of the wide variability of feeding rates among species of
261 different population sizes in a full community, instead of focusing on pairwise interactions with experimental
262 manipulation of a single resource density. We nonetheless expected to observe similar functional responses and
263 associated parameters since both approach describe the same underlying processes. Larger organisms are
264 expected to have larger space clearance rate, whereas handling time might vary with consumers and resource
265 body mass (Coblentz *et al.* 2023; DeLong 2021; Rall *et al.* 2012; Uiterwaal & DeLong 2020). Consistent with

266 the anticipated relationship, largest space clearance rate in model 2 are related to larger organisms such as large
267 and medium mammal predators, predatory birds and sharks, while lower space clearance rate are related to
268 smaller organisms such as invertebrates, shrimps and small pelagic fish omnivores (figure fig. 3). The space
269 clearance rate in model 3 mostly displays the same relationship with consumers body mass while having larger
270 flat distributions (figure fig. 3). The allometric relationship with handling time is however less precise, where
271 higher or lower handling time are not specifically related to larger or smaller organisms (figure fig. 3) Based on
272 field observations and modeling, handling time would not be as important in consumptions as resource
273 individuals needed to saturate a consumer's consumption rates could rarely be observed in natural context
274 (Beardsell *et al.* 2021; Coblenz *et al.* 2023; Preston *et al.* 2018). While not necessarily relevant in explaining
275 the poor unobserved body mass relationship of our handling time parameter, it might lend additional support for
276 model 2. Overall, the inter-consumer distribution of the space clearance rate parameter for model 2 and 3 fall
277 well within the range values reported in other studies (Coblenz *et al.* 2023; Portalier *et al.* 2022; Rall *et al.*
278 2012).

279 As with many other biological processes, feeding rates are tightly linked with consumers and resources body
280 mass (Brose 2010; DeLong 2021; DeLong & Vasseur 2012; Preston *et al.* 2018; Schneider *et al.* 2012;
281 Schröder *et al.* 2016). More specifically, the underlying space clearance rate and handling time parameters of
282 the feeding process are expected to scale with consumer body mass (DeLong 2021; Kalinkat *et al.* 2013;
283 Vucic-Pestic *et al.* 2010; Yodzis & Innes 1992). A review of several functional response studies summarized in
284 the foRAGE database (Uiterwaal *et al.* 2022) showed a clear allometric scaling relationship between consumers
285 body mass and space clearance rate among multiple taxonomic groups (DeLong 2021). The allometric scaling
286 of movement speed is hypothesized to be the mechanisms underlying variability in the relationship between
287 consumers body mass and their space clearance rate as it is a function of consumers velocity (DeLong 2021).
288 Maximum velocities were shown to be allometrically linked with their body mass, displaying a linear increase
289 on the log-scale up to certain extreme values of body mass (Bejan & Marden 2006; Hirt *et al.* 2017). The
290 estimates of the slope of this relationship however varies significantly between studies, with values that are
291 usually much smaller than 1 (Rall *et al.* 2012; **Delong2012DynExpa?**). We found an estimated slope of 0.98 on
292 the log-scale (figure fig. 5 -A), with a relatively narrow confidence interval, suggesting a linear relationship
293 between consumer body mass and the space clearance rate, which is coherent with a certain portion of the
294 relationship developed by Hirt *et al.* (2017). Although most of the consumers in model 2 seem to display the
295 expected relationship between space clearance rate and consumers body mass (figure fig. 5 -A), we can clearly

discern some species having an upward offset. The consumers of concern here are all terrestrial carnivores or omnivores belonging to the Arctic networks originating from the same set of study. As Ecopath compute estimates over a year step (Christensen *et al.* 2005; Christensen & Walters 2004) and the data from the Arctic networks were seasonally assessed for summer observations, we can not overlook that this offset might arise from a methodological bias. Alternatively, the higher space clearance rate of these terrestrial species might also arise from other impacting factors such as interaction dimensionality and habitat heterogeneity (Pawar *et al.* 2012). We also note that the allometric relationship disappears with the single-species saturating model (figure 5 -B-C). We believe this may happen because of a ridge in the likelihood space consequent to a tradeoff between space clearance rate and handling time, making the model non-identifiable. Perhaps this problem could be solved with stronger priors, for instance using parameters found in traditional functional studies such as Rall *et al.* (2012). Overall, the allometric relationship displayed in the consumer-specific mass action model represents another supporting element in favor of a simple mass-action model, which would significantly facilitates the parameterization of quantitative food web models.

Quantitative predictions: general extent, scope and limitations

Many techniques were proposed recently to infer ecological interactions from proxies (Morales-Castilla *et al.* 2015), some informed by theory (Portalier *et al.* 2019), others more flexible and using all of the information contained in the data (Strydom *et al.* 2021). These methods are motivated by on-going changes in biodiversity (Jordano 2016), urging for a more integrated description of community structure. There is however an inherent challenge in documenting interactions because their number scales with the square of species richness (MacDonald *et al.* 2020), some interactions are difficult to document (Poisot *et al.* 2021; Wootton & Emmerson 2005), and also because novel assemblages are made of species that were never seen co-occurring before (Lurgi *et al.* 2012; Montoya & Raffaelli 2010). The variety of available methods allow some flexibility, depending on the objective of the study and data availability. They are however all limited to binary interactions, i.e. if a pair of species are interacting or not. Quantitative information on the strength of interaction is required to move to a next stage of interpretation, just like abundance is a more accurate description of community structure than presence-absence. We successfully predicted biomass fluxes with a very limited amount of information which suggests that, paired with a method to predict binary interactions, the reconstruction of quantitative interaction networks is accessible. Our model analysis was inspired by theory, and despite a different methodological approach, our results are in agreement with previous meta-analyses of functional responses (Rall *et al.* 2012;

325 Uiterwaal & DeLong 2020), further strengthening the confidence in our models. We found also coherence in
326 parameter estimates across ecosystems and feeding guilds, suggesting that a general approach is within reach.
327 Nonetheless, although our models were built upon the best available data at the time, it should not be overlooked
328 that our results strongly depend on Ecopath model outputs, and thus their limitations. As such, the interpretation
329 of our results should reflect this reality. The obvious next step will be to catch some of the residual variance,
330 likely with the addition of other traits. Inspired by the methods used for binary interactions, the next model
331 generation will have to account for trait-matching between consumer and resource. Interactions could also be
332 made conditional on the environment, for instance on temperature affecting movement rates (Dell *et al.* 2014),
333 or the presence of refuges (Barrios-O'Neill *et al.* 2016; Chan *et al.* 2017). The parameterization we offered here
334 should eventually contribute to inform theoretical studies (Schneider *et al.* 2016) as well as global ecosystem
335 models that are developed to investigate the consequences of biodiversity changes (Harfoot *et al.* 2014).

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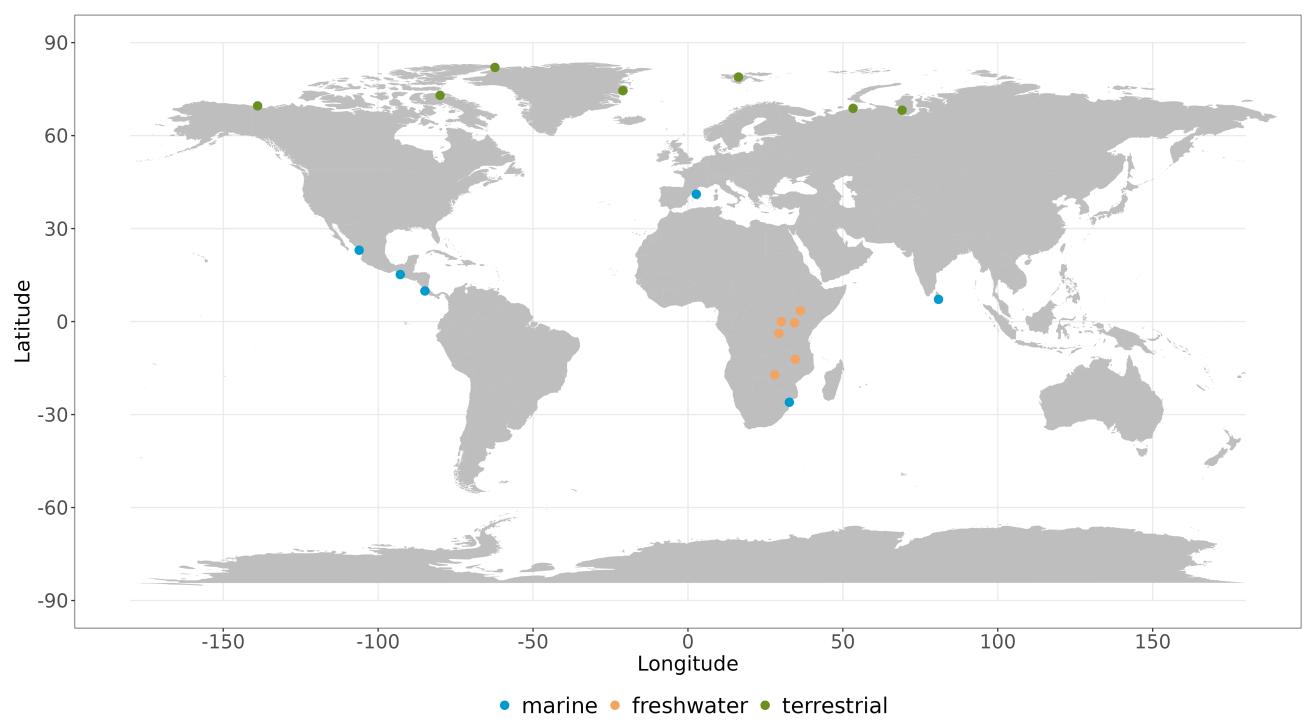


Figure 1: Map of Ecopath models locations used in the present study.

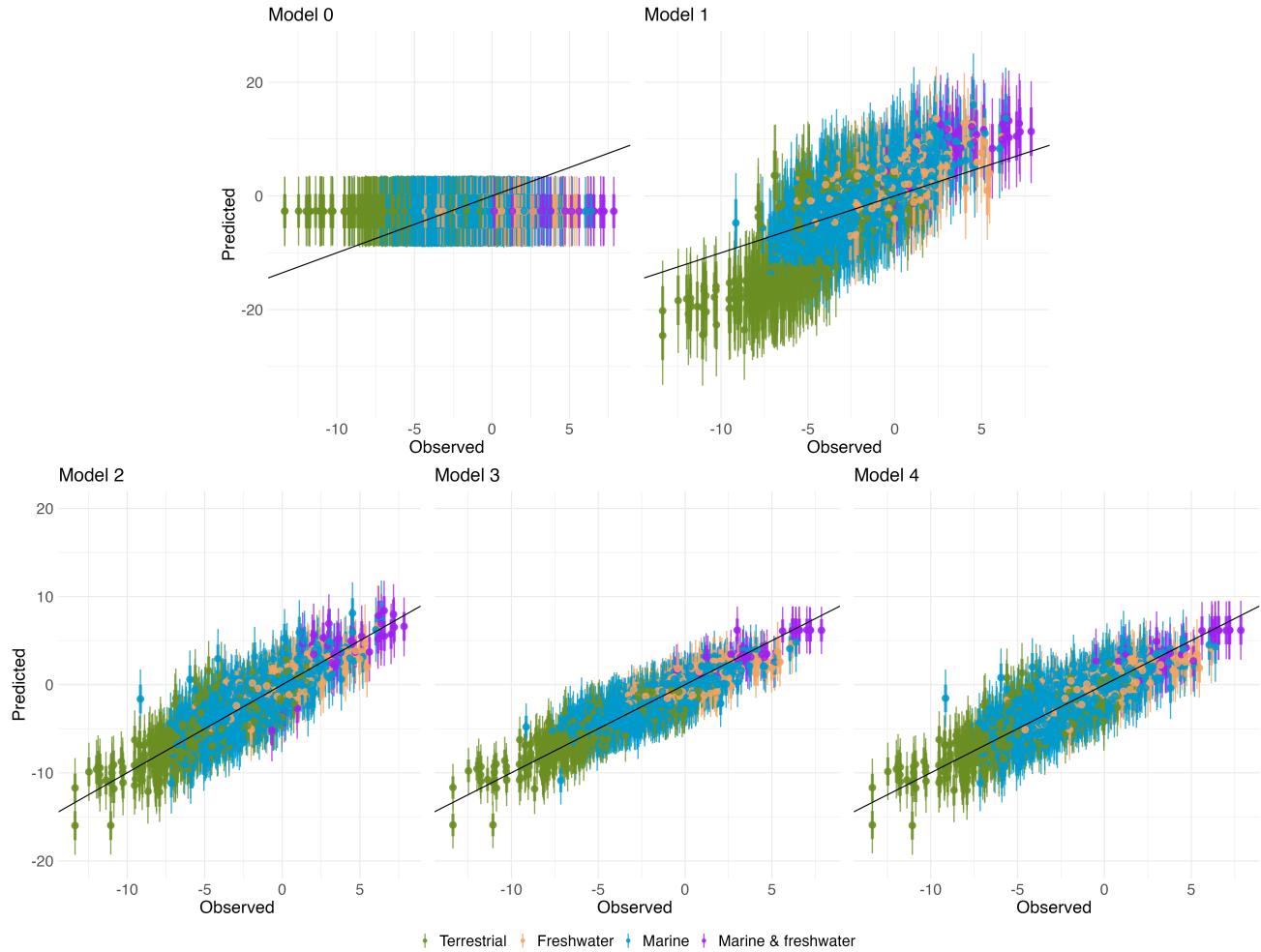


Figure 2: Models prediction of biomass fluxes compared to the observed biomass fluxes (log-scale) (metric tons/km²/year). The black line represents a one for one line. Points represent the mean predicted value and thick and fine error bars represent the 0.66 and 0.95 quantile distribution respectively. ‘Marine and freshwater’ points represent biomass fluxes from consumers that are present both in marine and freshwater ecosystems such as Zooplankton and Zoobenthos.

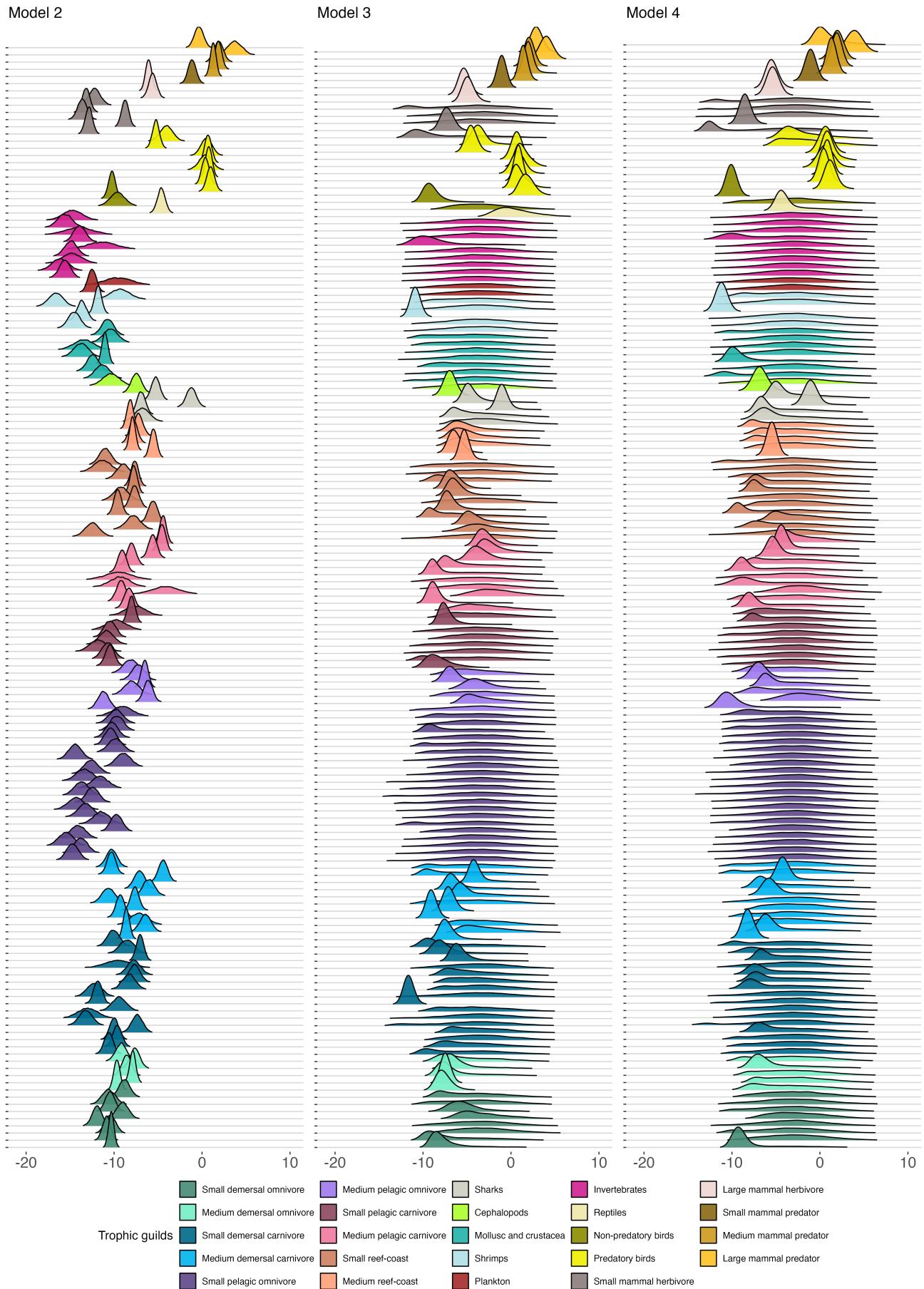
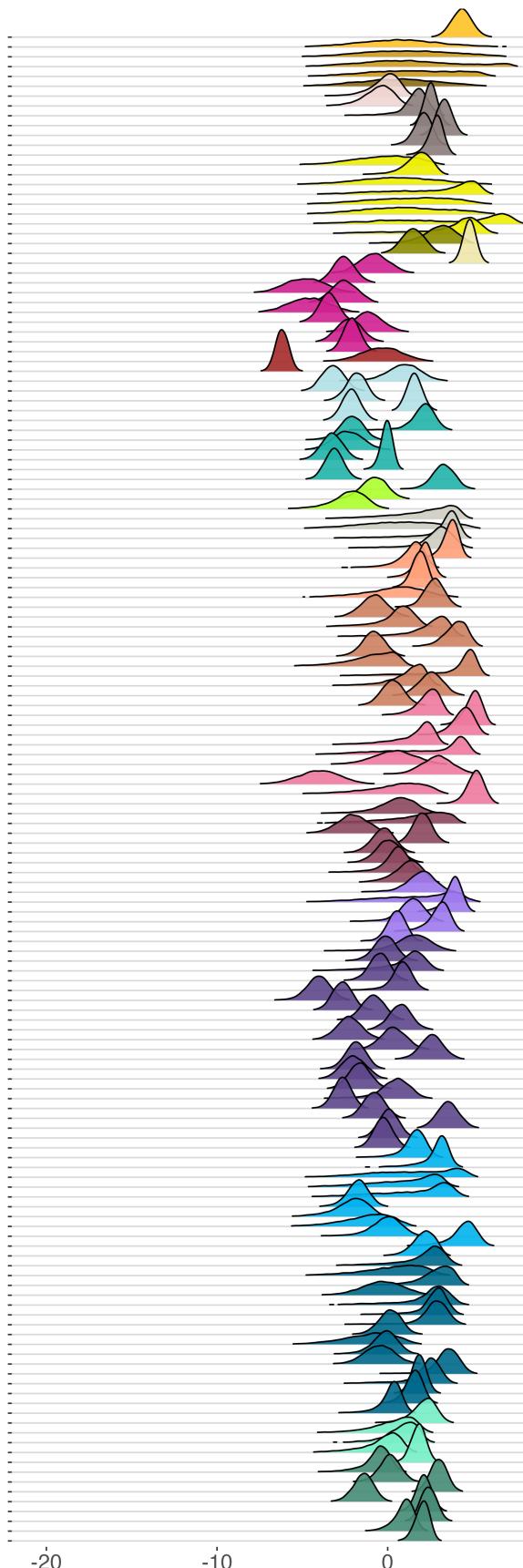
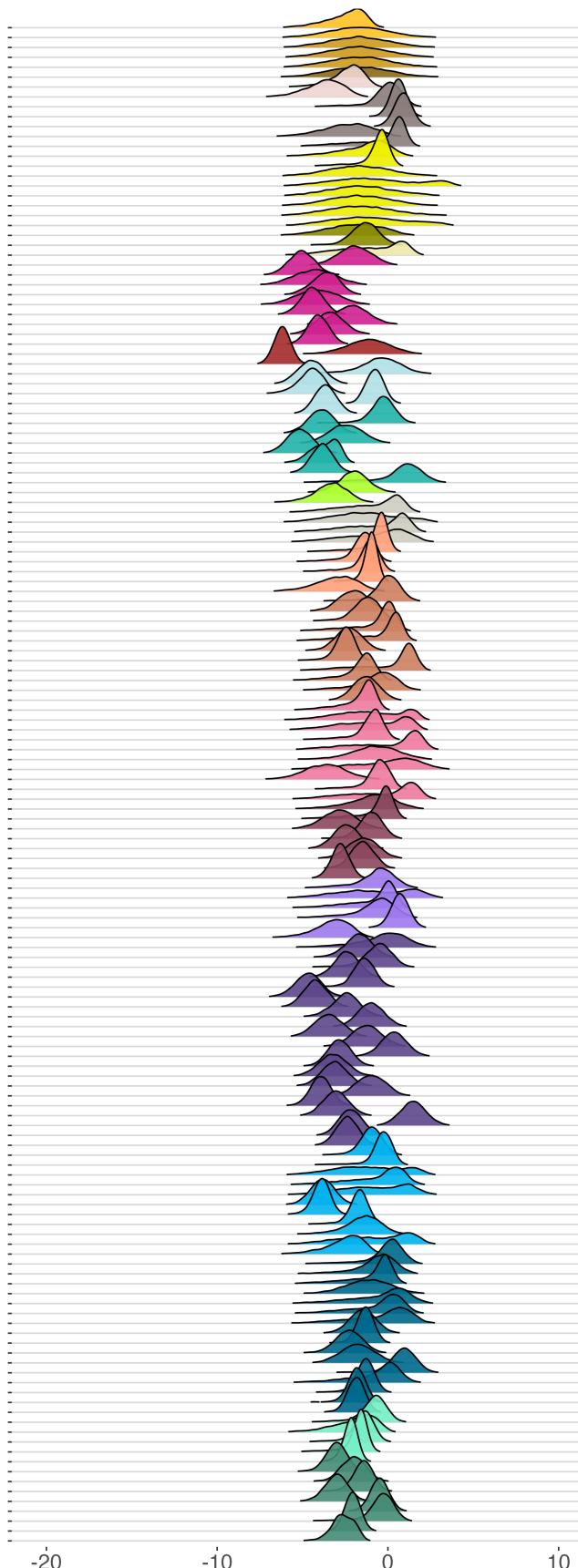


Figure 3: Posterior distribution of the space clearance rate parameter (log-scale) for model 2, 3 and 4 of 21

Model 3



Model 4



Small demersal omnivore	Medium pelagic omnivore	Sharks	Invertebrates	Large mammal herbivore
Medium demersal omnivore	Small pelagic carnivore	Cephalopods	Reptiles	Small mammal predator
Small demersal carnivore	Medium pelagic carnivore	Mollusc and crustacea	Non-predatory birds	Medium mammal predator
Medium demersal carnivore	Small reef-coast	Shrimps	Predatory birds	Large mammal predator
Small pelagic omnivore	Medium reef-coast	Plankton		Small mammal herbivore

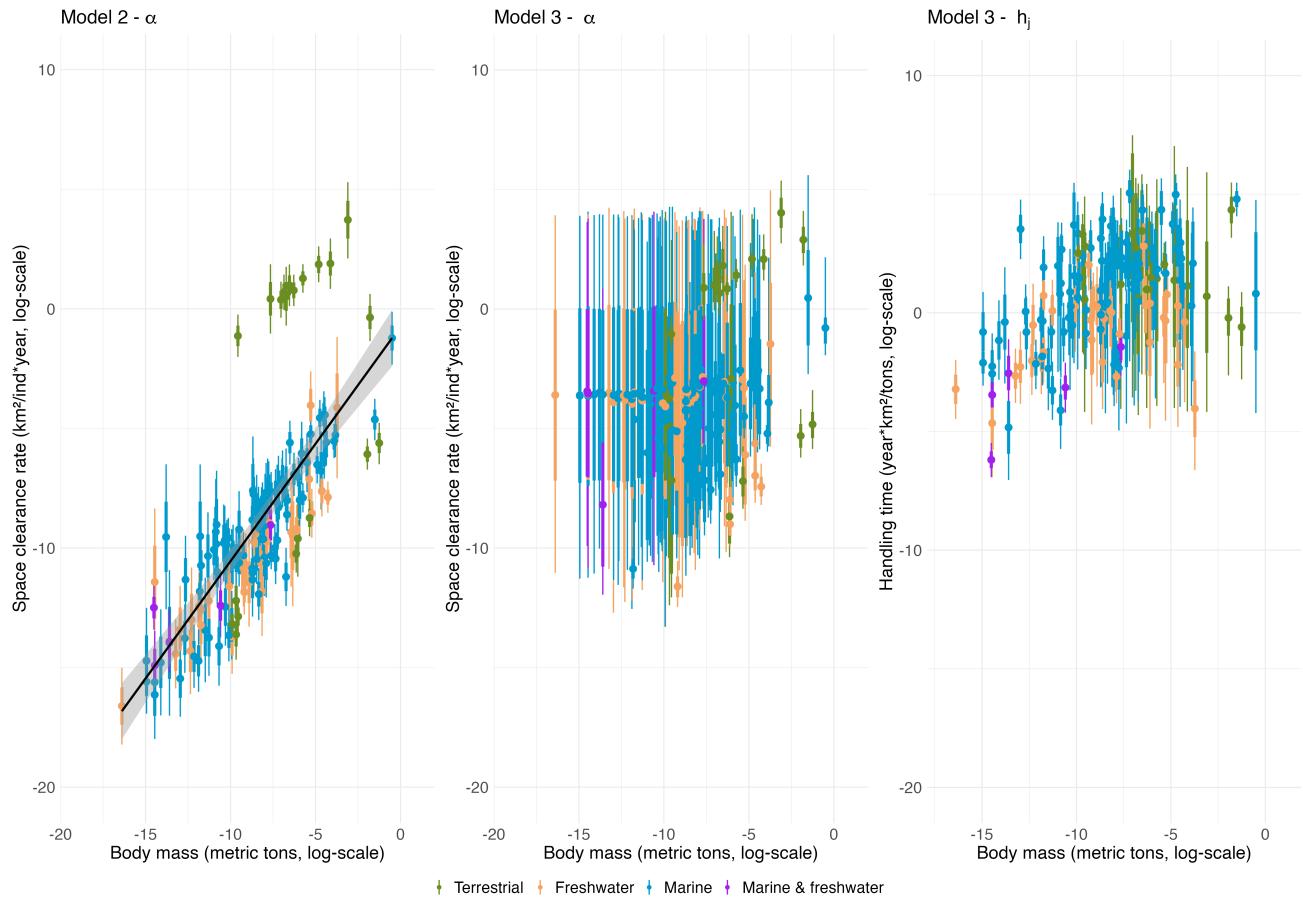


Figure 5: Relationships of the space clearance rate and handling time parameters with consumers body mass (log-scale). A clear and discernable relationship is present for model 2 space clearance rate and absent for model 3 space clearance rate and handling time parameters. The allometric relationship for model 2 space clearance rate is also accompanied by a linear regression with a slope of 0.98 (black line) and its 0.95% confidence interval (grey area). Points represent the mean space clearance rate and thick and fine error bars represent the 0.66 and 0.95 quantile distribution respectively.