**Reply to reviewers**

**# Reviewer 1**  
EVALUATION  
Please list your revision requests for the authors and provide your detailed comments, including highlighting limitations and strengths of the study and evaluating the validity of the results, and data interpretation. If you have additional comments based on Q2 and Q3 you can add them as well.  
1. Highlighting limitations and strengths of the study   
Authors used a novel mechanistic approach to infer size-based functional response to make explicit consideration of the movement of organisms in aquatic and terrestrial systems.   
However, the manuscript format is very casual and does not meet the basic requirements of this Journal. And the lack of some necessary elements of academic papers，and different elements are mixed up and confusing.

*We agree that the outline of the manuscript was not clear enough. We thoroughly modified it to make it clearer that it is a perspective paper. Following the editorial instructions, we discussed current advances and future directions by promoting a novel research avenue to investigate the functional response by including factors from the physical medium, and we included personal work (a derivation of the functional response from a published model) as an example of what can be done. We also tried to provide an accurate presentation and citations of other authors’ work in a clearer way. We also agree that the presentation of the results was not satisfactory. Thus, we added an evaluation of the goodness of fit of the model.*

2. Evaluating the validity of the results  
The authors propose new models for some existing problems raised by the research in the field, but the authors do not substantially verify the effectiveness of the model.  
The authors did not adopt a classical authoritative approach to verify the effectiveness of the model, for example, using statistical method degrees to validate the degree of compliance between predicted and actual values.

*We added several elements to evaluate the goodness of fit. First, we computed the root mean square deviation (RMSD) that account for the mean deviation of the predicted and observed data, as recommended in Pineiro et al 2008. Second, we added a test on the slope and intercept of the regression of observed versus predicted data (i.e., a slope of 1 and an intercept of 0 mean that the model is unbiased) with body size as a cofactor, and the source of data (i.e., the study where the data was originally collected) as a random factor. It appears that the slope and intercept of the regression for speed, attack rate and capture probability do not significantly differ from 1 and 0 respectively, with no significant effect of size nor the source of data. On the other hand, the model fails to accurately predict handling time, which is the only parameter that does not rely on mechanical factor in Portalier et al’s original model. Results can be found in the main text (l. 252-260 pp. 12-13, l. 297-315 pp. 14-15) and the full details can be found in the supplementary material.*

3. Data interpretation.  
The authors did not describe the results.

*With the addition of the measures for the goodness of fit, the validation of the results should be clearer. However, due to length constraints, we focused on the implications of the results in terms of theoretical advances or insights. More specifically, we discussed the fact that considering the mechanical factors from the medium leads to a good prediction of speed, attack rate and capture probability without the need for empirical measurements. Only handling time is poorly predicted, but it is also not affected by mechanical factors in the original model. More details on the results per se (i.e., how attack rate and handling time vary according to predator and prey sizes) can be found in the Supplementary material (Fig. S2).*

Detailed comments:  
Abstract:   
What is the aim of this work? What are the main results and conclusions of this work? I suggest that this information should be explicitly provided in the abstract section.  
*We thoroughly revised the abstract in order to make it clearer. In particular, we emphasized the fact that the aim of the study was to promote a novel approach to derive functional response by considering the physical properties of the surrounding medium. We also mentioned that our derivation from Portlier et al’s model that we proposed was a first attempt to achieve this goal, and that we used the results from the model to point out possible improvements.*

Introduction:  
What are the specific scientific problems proposed to solve in this work?  
What is the relationship in the following parts? For example, line 33 (Introduction), line 65 (Physical features of the medium and size-related constraints), line 129 (A case study as an example of new mechanistic approaches).

*We thoroughly revised the manuscript to make it clearer that the goal is to emphasize the need to include factors from the physical medium. The section “Empirical evidence of the impact of the physical properties of the medium on functional response” gives a general overview of factors from the medium that have been shown empirically to have effects on functional response. The section “Theoretical approaches to the role of physical features of the environment on predation” provides a review of former theoretical studies that took some aspects of the medium into account and their effects on predator-prey relationship. Last, in the section “A first case of an inferring of the functional response from the physical properties of the medium”, we present our model as a first step towards the goal presented in the previous section. We hope that this revised structure will make the manuscript clearer.*

Line117-124. The “novelty” and the “strength” related to the “approach” proposed by the authors, are the highlights of this work, and the author elaborated it is unpredictable, and it is necessary to elaborate in detail.  
*We provided more details on our derivation of the functional response from the original study (Portalier et al., 2019) (pp. 10-11). We also gave more information about the implications of the results (i.e., the fact that it is possible to derive attack rate and capture probability from body size and the physical components of the medium, but that it still needs further developments). We also discussed potential way to improve the model and future directions.*

A case study as an example of new mechanistic approaches  
What does this part do? What's the relationship with “Main framework”? Is the main framework affiliated with the author or the "case study"?

*We revised the structure of the manuscript. It should be clearer now that the model presented is a first attempt to achieve our goal. Even though we knew that further developments are needed before we can reach a sound physics-based functional response, we thought that it was important to show in this perspective paper, the potential of the approach with a first derivation from one of the most advanced models so far. We agree that the term “main framework” was misleading, thus we removed it. We also replaced the section title (“A case study as an example of new mechanistic approaches”) by “A first case of an inferring of the functional response from the physical properties of the medium”.*

The confusion arises follows:   
Are the equations (model) from 1 to 4 proposed by the authors or the "case study"?  
What is the foundation for proposing these models?

*Following our response to the former comment, it should be clearer now that the equations are the same as used in the Portalier et al.´s (2019) article that considers mechanical factors and body size in a predator-prey interaction. We also provided additional information about this model (pp. 10-11) so that the readers understand the assumptions and algorithms underlying our derivation of the functional response.*  
Validation of the model  
How to verify the effectiveness of the model? Are there some specific statistical methods to test the agreement between predicted and actual observations?

*As explained above, we computed the RMSD for each parameter, and we also tested for model bias by doing a test on the slope and intercept of the regression of observed versus predicted data for each parameter with body size as a cofactor (except for capture probability), and the source of data as a random factor (except for speed).*  
  
Discussion   
Discussions should be an important part of research papers. In terms of this work, it is necessary for the authors to discuss the ecological significance of the established model and its application value deeply.

*We developed the validation and conclusion sections to emphasize the insights that one can get from this kind of approach. We also discussed potential improvements to the model and ways to push this approach further.*

Animal size is affected by developmental stages as well as contaminants. How will these factors be taken into account in building the models? What are the use scope and limitations of this model? These issues are necessary to be fully discussed.  
However, this manuscript does not contain this part.

*Portalier et al’s 2019 model considers size as the main trait characterising organisms. Thus, two individuals taken at two different development stages (for example) would behave differently as long as they differ in size. On the other hand, two individuals at two different stages but of the same size would be considered as similar.*

Conclusions  
The conclusion part should be a concise summary of the experimental results, rather than to discuss.

*We revised the conclusion to emphasize the potential insights that one can get from the novel approach that the model illustrates.*

**# Reviewer 2**EVALUATION  
Please list your revision requests for the authors and provide your detailed comments, including highlighting limitations and strengths of the study and evaluating the validity of the results, and data interpretation. If you have additional comments based on Q2 and Q3 you can add them as well.  
General Evaluation:  
Main findings of the manuscript  
The authors aim to improve our understanding of the predator-prey relationship by including an explicit consideration of the movement of the organisms involved, and hence of mechanics. They provide a model that derives classical parameters of a functional response from body size or organisms involved and physical factors of the medium, which can be easily measured. The novelty is that parameters are not estimated from observational predation data.  
  
Limitations:   
Some wording could be changed for clarity and brevity. In addition, the authors need to provide quantitative data on the model fits, and need to better highlight the novelty of the study.   
*As mentioned in the reply to reviewer 1, we added several elements to evaluate the goodness of fit. First, we computed the root mean square deviation (RMSD) that account for the mean deviation of the predicted and observed data. Second, we added a test on the slope and intercept of the regression of observed versus predicted data (i.e., a slope of 1 and an intercept of 0 mean that the model is unbiased) with body size as a cofactor, and the source of data (i.e., the study where the data was originally collected) as a random variable. It appears that the slope and intercept of the regression for speed, attack rate and capture probability do not significantly differ from 1 and 0 respectively, with no significant effect of size nor the source of data. On the other hand, the model fails to accurately predict handling time, which is the only parameter that does not rely on mechanical factor in our model. Results can be found in the main text (l. 252-260 pp. 12-13, l. 297-315 pp. 14-15) and the full details can be found in the supplementary material.*

Strengths:  
Provision of a model that derives classical parameters of a functional response from the easily measured parameters body size and physical factors. Use of the model means that the parameters so not need to be estimated from observational predation data.  
  
Specific Evaluation:  
Title:  
1) Line 1: Can “biomechanical” be changed to something more informative? Line 100 talks about physical properties, which seems like it should be in the title.

We changed the title accordingly. The title is now: “Inferring size-based functional responses from the physical properties of the medium”.

Introduction:  
2) Lines 52-58: Has this relationship of the FR to size already been well established? Need to focus on the novelty of this study.

*We edited the paragraph accordingly (l. 80-87 p.4). We explained that our understanding of this well-known relationship would be improved by incorporating the physical medium in models, since its effects mostly vary with size.*

3) Lines 55-58: Could add more references from the marine realm in addition to Williams et al., such as Miller, T. J., Crowder, L. B., Rice, J. A., & Binkowski, F. P. (1992). Body size and the ontogeny of the functional response in fishes. Canadian Journal of Fisheries and Aquatic Sciences, 49(4), 805-812.

*We added the corresponding reference.*

4) Lines 85-88: Seems like body size VERSUS viscosity should matter in the model.

*We clarified this point (l. 144-145 p. 7).*

5) Line 94: Add references after “promising avenue.”

*Actually, the references were the topic of the remaining of the paragraph. However, we agree that it was misleading. Thus, we made it clearer (l. 154).*

6) Lines 94-95: Seems like many of the concepts presented in this paper have been described elsewhere, so authors need to highlight the novelty of this study.

*We added a couple of sentences to clarify this point (lines 178-181 p. 10).*

7) Lines 100-101: The use of the words “physical properties of the medium” would be informative to list in the title.

*We changed the title accordingly. The title is now: “Inferring size-based functional responses from the physical properties of the medium”.*

8) Line 105 (and elsewhere): Don’t forget the period and comma after “et al”.

*We corrected these typographic errors.*

9) Line 122: Clarify what is meant by “…attack rate and handling time would become emerging properties of the model.”

*Due to the revisions, this sentence has been removed. However, a clearer formulation can be found in the conclusion (l. 370-371 p. 18).*

10) Line 127: Should add “and the medium” (or some such statement) after “related to body size” (because it’s not JUST body size that is being considered).

*We followed the suggestion.*

11) Line 132: Can authors give a quantitative value for what they mean by “fits data remarkably well”?

*The original model by Portalier et al (2019) predicts a range of prey sizes that a given predator can prey upon in a sustainable way (i.e., the capture is successful, and the energetic reward is greater than the energetic expense). Therefore, we cannot do the same test as we do in the current manuscript. However, in the original study (Portalier et al., 2019), in pelagic systems, and for predators that meet the assumptions of the model, 80% (for species-based data) and 90% (for individual-based data) of observed predator-prey interactions fall into the predicted rage of prey sizes. We added this piece of information in the manuscript (l. 208-209 p. 10). Moreover, predictions of food web structure for 10 pelagic food webs were compared to predictions by the allometric niche model using the True Skills Statistics (Portalier et al 2019). Portalier et al’s model proved much more accurate. However, for brevity reasons, we do not discuss those results in the current manuscript.*

12) Line 136: Unclear which model is meant by “this model”. The one in Portalier 2019 or the one in the current ms?  
*It is the Portalier et al. (2019) model. We clarified this point.*

Main framework & Validation of the model  
13) Line 140: The addition of “physical features” should be highlighted.

*We modified the paragraph as suggested (l. 223-229 p. 11).*

14) Line 164: Can authors add a quantitative way to look at how well the model fits the data?

*We replied to this comment in details above. For each parameter (speed, attack rate, capture probability and handling time), we computed a RMSD and we tested if the slope and intercept of the regression between observed and predicted data significantly differ from 1 and 0 respectively.*

15) Line 184: Shouldn't the equations allow for type III FR also?

*Yes, equation 4 could allow for a type-III. In Portalier et al. (2019), the encounter rate model used leads to a type-II. But if another encounter rate model is used, we could compute a type-III functional response. We clarify this point in the manuscript (l. 284-289 p. 14).*

16) Line 188: For brevity, remove “in order”.

*We removed “in order”.*

17) Lines 189-190: Seems like personal notes that should be removed.

*The reviewer is right. We removed this point.*

18) Line 194: “It appears that the model fits the data quite well” is not at all convincing. Need a quantitative measure of model fit (e.g., goodness of fit, residuals, model skill).

*We replied to this question above. We computed a RMSD and we tested the slope and intercept of the regression between observed and predicted data.*

19) Line 195: Seems like there are quite a lot of data for organisms in the mg size range and below, so this is not a valid reason. Seems like the model needs to change to include small organisms.

*We agree with the reviewer that the argument was not valid. Actually, the statistical analysis does not show any significant bias for attack rate according to size. Thus, our former comment (in the former version of the manuscript) is not valid anymore.*

20) Line 197: Handling time is very far off and the model for this needs to be changed.

*We changed the sentence. The end of the corresponding paragraph discusses the fact that handling time is not related to mechanical factors from the medium in our model, and thus Portlier et al’s model should be revised to better model handling time.*  
Conclusions and future directions  
21) Line 206: Not convinced that this model is useful for this type of prediction.

*We agree that the sentence was misleading. Our point was to provide some potential improvements for the model. We made it clearer (l. 321-322 p. 15).*

22) Line 221: Again, not convincing to just state that the model fits data well. Model may be of little value if authors cannot quantitatively demonstrate that the model processes fit real data well.  
*We replied to this question above. We computed a RMSD and we tested the slope and intercept of the regression between observed and predicted data.*

Figures  
23) Line 392: The relationship of the real data looks like it could be modeled as a sigmoid function in Figure 1.

*Our model tries to be general across a wide range of sizes. However, it is possible that small organisms experience supplementary constraints that are not included in the model, which results in an overestimate of their speed. Similarly, larger animals may show specific adaptations (such as lubrification of the body) that increase their speed, and that are not size-related. These factors were not included in the original model model by Portalier et al (2019). They should certainly in the future.*

24) Line 396: Can something be added to have the model asymptote at large sizes?

*See answer to previous comment.*

25) Lines 399-400: This wording is repetitive of what's in the text and can be removed here.  
*We removed this sentence.*

Concluding Remarks:  
Authors need to focus on highlighting the novelty of the study and also providing quantitative evidence of model fit to convince the reader.  
*We hope that the revised manuscript successfully addresses these remarks.*

**# Reviewer 3**  
EVALUATION  
Please list your revision requests for the authors and provide your detailed comments, including highlighting limitations and strengths of the study and evaluating the validity of the results, and data interpretation. If you have additional comments based on Q2 and Q3 you can add them as well.  
General comment:  
In this manuscript the authors present a model that derives functional response parameters from allometric relationships of predators and prey and physical properties of the surrounding medium. The model is tested against published data from two recent meta-studies and a couple of additional original studies.   
I think this is an interesting study but I have a few major concerns and also a couple of minor comments about this manuscript that need to be addressed to improve its quality and comprehensibility. See my comments below. Overall I think this will be a valuable contribution to the field after a solid revision.   
General suggestions:   
One think that was not really clear to me and which I think is most important for the overall evaluation: how is this new study related to the previous study Portalier et al (2019)? Which parts of the model framework are maintained compared to this study and what part is truly novel here in the new paper? It seems that the consideration of the physical properties of the medium should be the novel part now but some considerations to this respect have been included in the previous study as well, as far as I understand.

*The current study actually dos not add to Portalier et al’s model. Rather, it uses the original equations to derive the parameters of the functional response. The original model computes time expenditure (for searching, capturing and handling) and energetic expenditure. The present model uses only part of the original one to compute time expenditure. We clarified this point (l. 223-229 p. 11).*

Moreover, I found that considerable parts of the relevant literature need to be considered (and cited) in the revised manuscript, see detailed examples below.

*We added several references, following the reviewer’s suggestions.*

A minor general point that I see missing from the discussion is the differentiation between foraging modes of predators. There are numerous studies that consider sit-and-wait predators versus actively foraging predators in the context of functional response studies (e.g. Twardochleb et al. 2020). In these either prey or predator velocity are main drivers of interactions. I think this has important implications for the model presented in your study and the underlying mechanisms need to be discussed here.

*We added a paragraph to address this point in the conclusion section (l. 360-367 p. 17). The model assumes that both the predator and its prey move and can detect each other without any interference. This does not hold for sit-and-wait predators. The model can be adapted to compute an encounter rate in the case of a moving prey and a non-moving predator, but behavioral aspects such as hiding are not size-related, and therefore are not included in the model, although it could be a potential way to improve it.*

Specific suggestions:   
p.2 l.37: I would suggest to cite one of the earlier papers by Holling here, i.e. (Holling 1959)

*We added the reference.*

p.4 l.68: also see (Pawar et al. 2015)

*We added the citation.*

p.4 l.68: I suggest to write “or habitat complexity (Barrios ...)” or alternatively “or structural complexity (Barrios ...)”

*We added “habitat complexity”.*

p.4/5 ls.78-91: for the whole paragraph please also consider the publications by Beveridge and colleagues (Beveridge et al. 2010a, b) which seem very relevant in several aspects of this work.

*These two papers are relevant indeed. They are now cited in the corresponding paragraph.*

p.5 l.98: (Pawar et al. 2019) is not listed in the bibliography

*We added the full reference.*

p.5 l.99: maybe also consider the very recent publication by Cloyed and colleagues here (Cloyed et al. 2021)

*We added the reference.*

p.7 l.138: by giving this explicit reference to pelagic organisms do you mean the model does perform worse for all other kinds of interaction types? This is also relevant in terms of the Pawar et al (2012) terminology where pelagic interactions as 3D/3D interactions are different than 2D/3D or 2D/3D interactions. Should be considered.

*The model assumes that both predator and prey move within the fluid, and cannot hide from one another. This affects the equation used to calculate encounter rates. This is why the model is well-suited for pelagic or flying organisms. Interactions occurring on the bottom of the system (i.e., benthic or terrestrial systems) violate these. We clarified this point in the corresponding paragraph. Inclusion of dimensionality into Portalier et al’s model seems the next natural step to undergo within the physics-based approach that we advocate.*

p.9 l.176: At least for ectotherms digestion is not independent from the physical property temperature (Rall et al. 2012). As you point out correctly, digestion is an integral part of the mechanisms subsumed in the handling time parameter. Please clarify.

*We agree with reviewer that this point needed clarification. We meant that it is independent of the mechanical factors included in the model (i.e., gravity, density, viscosity). We clarify this point in the corresponding paragraph (lines 273-276 p. 13).*

p.9 ls.189/190: this seems like instructions from authors to authors themselves. This needs to be cleaned up!

*The reviewer is totally right. We removed this part.*

p.9 l.190: I see that the references are listed in the data files on GitHub but why not include them in the supplementary materials?

*We added the full references in the Supplementary material.*

p.11 l.233: please also add (Jeschke 2007)

*We added the reference.*

**# Associate editor**

Dear Dr Portalier,   
  
The paper has now been reviewed by three reviewers. I agree with Reviewers 2 and 3 in that this manuscript has the potential to be a valuable and interesting contribution, but that substantial revision is required.  
  
Specifically, I agree with Reviewers 1 and 2 in that the manuscript requires quantification of the model fits. While the text and figures are helpful for describing and depicting the general trends, at this stage there is no quantification of how well the modeled parameters match the empirical data which significantly weakens the model validation section of the manuscript.

*We added several elements to evaluate the goodness of fit. First, we computed the root mean square deviation (RMSD) that account for the mean deviation of the predicted and observed data. Second, we added a test on the slope and intercept of the regression of observed versus predicted data (i.e., a slope of 1 and an intercept of 0 mean that the model is unbiased) with body size as a cofactor, and the source of data (i.e., the study where the data was originally collected) as a random variable. It appears that the slope and intercept of the regression for speed, attack rate and capture probability do not significantly differ from 1 and 0 respectively, with no significant effect of size nor the source of data. On the other hand, the model fails to accurately predict handling time, which is the only parameter that does not rely on mechanical factor in our model. Results can be found in the main text (l. 252-260 pp. 12-13, l. 297-315 pp. 14-15) and the full details can be found in the supplementary material.*

Please ensure that you provide a complete list of references where you obtained the data for model validation in your Supplementary Material (Line 189-190).   
*We added the full references in the Supplementary material.*

In addition, Reviewer 3 points out a substantial amount of relevant literature that should be considered (and cited) in the revised manuscript. This reviewer further points out that predator foraging strategy (sit-and-wait vs. active foraging) can substantially impact the functional response, which likely has substantial implications for the model presented in this manuscript. For example, depending on predator foraging mode it may be that prey or predator velocity is the main driver of the interaction. Please take some time to review the list of papers provided, and, where appropriate, incorporate some discussion of additional factors not considered in your model that may be relevant.

*We followed suggestion from reviewer 3. We added the relevant literature suggested, and we added a paragraph to discuss the case of sit-and-wait predators.*  
  
Each of the reviewers pointed out that the novelty of this work could be better articulated. Reviewer 3 has specifically asked that you address how this work relates to the previous study Portalier et al (2019), and how the material presented here is novel relative to the processes modeled in that paper.

*We clarified this point.*  
  
Below I have included a few additional comments / questions of my own:  
  
The effects of predator density on a predator’s per capita kill rate are now generally thought to be widespread. This mechanism is mentioned only in pasting towards the end of the manuscript (line 239-241). I agree that one could include other aspects associated to predation such as behavioral features into the model, but the reader is left wondering how this might be done or how it would improve model predictions. Which biological features specifically do you anticipate being important in reconciling the discrepancy between the predicted / observed data you present, and why? My suggestion is that you consider briefly describing how incorporating the biological part (e.g., interference) could help explain discrepancies in observed vs. predicted parameters, and /or be built into this modelling framework.

*As comes out of the manuscript, the first improvement to the model to enact would be to include better mechanism for handling time (especially prey subjugation, and predator satiation). Inclusion of dimensionality, as in Pawar et al (2012) is also among the first improvements to make. We agree that there is the need to include interference between predators. There is certainly a way to do this according to a very similar approach, probably by calculating encounter rates based on the relative speed of the 2 predators, and “capture” and “escape” probabilities as well, and add a time penalty for these encounters in our time-based functional response derivation. However, we felt that the scope and space of this manuscript would not allow to elaborate on this potential development of the theory in a good way. If length limitations are not a stringent constraint, we are happy to include such considerations in the manuscript in a future revision.*  
  
Within the proposed framework the functional response behaves as a Type II response, yet we know that other forms of the functional response better match empirical data sets. Interestingly, there has been some recent work indicating that crustaceans exhibit nearly double the proportion of sigmoidal functional responses (Holling type III) as compared to predatory fishes (Dunn and Hovel 2020 Biol Lett). To what extent could the discrepancy in observed vs. predicted handling times be related to taxonomic differences (e.g., invertebrate / vertebrate)?

*It is possible that anatomic/physiological differences that affect motion play a role (e.g., fish fins do not behave exactly like flagella). However, the goodness of fit analysis did not reveal any significant bias for speed, which is the core of the model, nor for attack rate according to body size. More importantly, the source of data (i.e., the study where the data comes from) does not have a significant effect on the goodness of fit for attack rate nor for handling time. Since these studies were usually done on specific taxa, we can reasonably infer that it is a proof (although indirect) that there was no major difference due to taxonomy. Due to length limitation, we did not develop this point in the main text.*

Moreover, Vucic-Pestic et al (2009) found that variation in predator–prey body-mass ratios could also impact the shape of the functional response (Type II vs. Type III). I think there would be value in briefly discussing if / how your framework might be revised to consider distinct functional response shapes (e.g., by altering assumptions within the underlying model).

*We agree that other types of functional responses should be considered (as reviewer 2 also mentioned). Actually, the model uses an encounter rate model from the literature (Rothschild and Osborn, 1988). This model leads to a type-II functional response. Another encounter rate model would lead to another type of functional response. We addressed this comment in the revised manuscript (l. 285-287 p. 14).*