A biomechanical approach to infer size-based functional response in aquatic and terrestrial systems

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Conflict of interest statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Author contribution statement

S.P. led the writing of the manuscript, implemented the model, gathered data, and performed simulations and analysis. M.C., G.F. and M.L. provided conceptual advices and guidance. All authors discussed the results and contributed equally to earlier drafts.

Keywords

Abstract

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First derivations of predators' functional response were mechanistic, but subsequent uses of these mechanistically-derived functions tended to be mostly phenomenological. A better understanding of mechanisms underpinning the functional response might lead to novel insights into predator-prey relationships in natural systems. Here we use a novel mechanistic approach that makes explicit consideration of the movement of organisms. Living organisms are constrained by the physical properties of their surrounding medium. In particular, these physical properties, mediated by body size, constrain the ability of both predators and prey to move, and thus affect the functional response. As an example of this approach, we build a model that derives classical parameters of the functional response (i.e., attack rate and handling time) from body size and physical factors. The novelty of this approach is that parameters are not estimated from observational data. The model only needs data on body size and physical properties of the medium, which can be easily measured. Our approach also provides easy ways to validate or falsify hypotheses about predator-prey relationships because discrepancies between predictions and real data point immediately to either errors in the model or missing mechanisms.

Contribution to the field

Functional response commonly describes predator and prey interactions. A growing body of literature shows that living organisms are constrained by the physical properties of the surrounding medium. We propose 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. The ability of moving, to search and capture a prey, is essential for most predators. Motion is affected by physical properties, in relation with body size. Considering mechanical effects from the medium grounds the functional response within its physical, local environment, and makes it dependent on measurable morphological traits and physical features. As an example of this kind of approach, we provide a model that derives classical parameters of a functional response from body size and physical factors, which can be easily measured. The novelty is that parameters are not estimated from observational predation data. This approach also provides easy ways to validate of falsify hypothesis. Hence, discrepancies between predictions and observations point immediately towards an error in the modelling, or means that important mechanisms are missing. Hence, measures done at the organismal level lead to patterns at the community level.

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2 **and terrestrial systems**

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Abstract

First derivations of predators' functional response were mechanistic, but subsequent uses of these mechanistically-derived functions tended to be mostly phenomenological. A better understanding of mechanisms underpinning the functional response might lead to novel insights into predator-prey relationships in natural systems. Here we use a novel mechanistic approach that makes explicit consideration of the movement of organisms. Living organisms are constrained by the physical properties of their surrounding medium. In particular, these physical properties, mediated by body size, constrain the ability of both predators and prey to move, and thus affect the functional response. As an example of this approach, we build a model that derives classical parameters of the functional response (i.e., attack rate and handling time) from body size and physical factors. The novelty of this approach is that parameters are not estimated from observational data. The model only needs data on body size and physical properties of the medium, which can be easily measured. Our approach also provides easy ways to validate or falsify hypotheses about predator-prey relationships because discrepancies between predictions and real data point immediately to either errors in the model or missing mechanisms.

Keywords: functional response, predator, prey, medium, body size, mechanics

Introduction

The study of prey consumption by a predator (i.e., the functional response) began several decades ago (Gause, 1934; Gause et al., 1936) and was accompanied by the development of a theoretical framework based on mechanistic principles (Lotka, 1923; Volterra, 1926; Beverton and Holt, 1957; Watt, 1959). The model proposed by Holling (1961; 1966) is one of the best known. This mechanistic model defines parameters such as attack rate (the rate at which a predator encounters

39 and captures prey) and handling time (the time needed by the predator to subdue, ingest and

40 digest the captured prey, and during which the predator cannot attack another prey). These

41 parameters can be measured concomitantly, and they give information about factors that

42 constrain predation on a given prey, which is a strength of this mechanistic approach.

43   Holling's type-I, II and III models and subsequently derived models (e.g., Rogers (1972))

44 are still widely used as a framework to derive the values of attack rate and handling time from

45 empirical data (e.g., Andresen and van der Meer, 2010; Farhadi et al., 2010; Papanikolaou et al.,

46 2011)). These approaches give valuable information on the studied systems, and they allow

47 hypothesis testing, such as the effects of temperature (Archer et al., 2019) and predator satiation

48 (Li et al., 2018) on the functional response. However, these studies have been mostly carried out

49 in the laboratory, where many external factors do not play a role (Abrams, 1982). Hence, the

50 results are hard to generalise and transpose to natural situations. Nonetheless, Holling's model

51 has been a very successful approach founded on mechanistic principles.

52   Several studies have investigated the role played by specific factors known to affect the

53 functional response. These models have emphasized different features of predator-prey

54 relationships, such as feeding saturation (DeAngelis et al., 1975) and interactions between

55 predators (Beddington, 1975; Sih, 1979). In particular, the body size of both predator and prey

56 are known to strongly affect the functional response (Aljetlawi et al., 2004; Vucic-Pestic et al.,

57 2010). Body size is a good predictor of trophic position (Williams et al., 2010) and affects the

58 overall dynamics of the interaction (Yodzis and Innes, 1992).

59   However, the surrounding physical medium remains absent or, at least, only implicit in most

60 models, despite its ubiquity in real ecosystems. Although, in his pioneer work, Tansley (1935)

61 stated that organisms should not be separated from their "special environment, with which they

62 form one physical system", the role played by the physical medium in constraining the functional

63 response remains largely unexplored. Including physical features into predator-prey models is

64 likely to lead to novel insights about species interactions.

Physical features of the medium and size-related constraints

66   Previous studies that have considered the surrounding medium have usually focused on

67 specific aspects of predation or on specific taxa (Domenici et al., 2011), or have investigated one

68 specific aspect of the medium such as dimensionality (Pawar et al., 2012) or complexity (Barrios-

69 O'Neill et al., 2016). But the overall role played by the surrounding medium acting on the

70 predator-prey relationship, which drives the functional response, remains to be explored.

71   Clearly, living organisms are constrained by the physical properties of the surrounding

72 medium (Denny, 1993; Denny, 2016; Vogel, 1996). These properties affect the way organisms

73 move and/or interact with each other in different ways. For example, in aquatic systems, turbidity

74 is an essential factor for predator or prey that rely on visual cues to detect each other (Martens et

75 al., 2015). Another example is turbulence, which controls many planktonic organisms'

76 suspension within the water column (Rodríguez et al., 2001) and affects contact rate between

77 predators and prey (Kiørboe and Saiz, 1995).

78   An important aspect of mechanical factors (i.e., gravity, density and viscosity) is that they

79 constrain motion. Aquatic organisms do not experience the effects of gravity as terrestrial

80 organisms usually do because the medium density is much higher in water than in air, which

81 creates higher buoyancy. Since predation usually implies motion, these factors create mechanical

82 constraints acting differently on predators in different physical environments. These mechanical

83 factors are ubiquitous, affect small (Kiørboe and Saiz, 1995) as well as large predators (Howland,

84 1974; Domenici et al., 2007) and are usually size-dependent. In particular, medium viscosity and

85 density affect species' motion through drag, which is why the motion of planktonic organisms

86 has very different features than that of larger organisms. Metrics such as the Reynolds number

87 are commonly used to discriminate between organisms that experience viscous drag (low

88 Reynolds number) and those that experience high inertia (high Reynolds number). These features

89 affect species according to their size and shape (Koehl and Strickier, 1981; Koehl, 1996). Thus,

90 incorporating mechanical constraints into models could lead to a better understanding of the size-

91 based relationship between predators and prey, and hence of the size structure of food webs.

92   Due to this size dependence, models incorporating physical (including mechanical) factors

93 into predation merge size-related biological and mechanical constraints in classical predator-prey

94 systems. Several studies have begun to investigate this promising avenue. The dimensionality of

95 the physical medium was shown to constrain predator-prey interactions since predators are

96 expected to capture pelagic and flying prey more efficiently than benthic and terrestrial prey

97 (Pawar et al., 2012). Extending this framework to predict pairwise trophic interactions in natural

98 situations, Pawar et al (2019) successfully reproduced some important differences in the

99 consumer-resource size structure of 2D versus 3D communities. However, dimensionality is only

100 one feature of the physical medium. Some studies coupled several physical properties of the

101 medium simultaneously in a plankton model (Baird and Emsley, 1999), including their effects on

102 different resource-use strategies, such as photosynthesis, nutrient uptake and predation (Baird et

103 al., 2006). Addition of these biomechanical mechanisms correctly predicted emergent ecosystem

104 properties, such as deep chlorophyll maxima, where non-biomechanical models were unable to

105 do so (Baird et al 2004). This additional realism was due specifically to the inclusion of effects of

106 hydromechanical processes such as advection and turbulent dissipation on planktonic organisms

107 (Baird et al 2004, 2006). This kind of approach was later extended to marine food webs using an

108 oceanographic model, which proved interesting in its capacity to generate realistic food webs

109 with relatively few generic rules (Baird and Suthers, 2007). But the validation of the model

110 assumptions at a scale smaller than the ecosystem was less successful, due to the small size of

111 planktonic organisms, and the scale at which the model was applied (ocean basins and currents).

112 Similarly, a framework for predicting the optimal motion of larger organisms as a function of size

113 and internal and external factors is under development (Wilson et al., 2015, 2013). The

114 importance of physical factors in determining motion has been acknowledged (Wilson et al.,

115 2015), but their explicit and quantitative inclusion in this framework has started only very

116 recently (Portalier et al 2019).

117   The main advantage of many models coupling physical and general biological laws is that

118 parameters in the models are mostly related to the body size of predators and prey, a trait that is

119 commonly measured, which makes predictions from the models easily testable. Applying this

120 approach to the study of the functional response would allow for a real novelty since the

121 parameters of the functional response would no longer be measured at the community level, but

122 would be derived from the individual (or species) level. Classical parameters such as attack rate

123 and handling time would become emerging properties of the model. Another strength of this

124 approach is that it allows hypothesis testing, since discrepancies between predicted and observed

125 patterns would point to incomplete or erroneous hypotheses.

126   In order to illustrate this novel approach, we propose to include some of the mechanical

127 factors related to body size in a theoretical model that predicts the functional response of a given

128 predator consuming a given prey.

A case study as an example of new mechanistic approaches

In a recent study, Portalier et al. (2019) provided a biomechanical model that uses general laws of mechanics and well-known biological laws, all related to body size, to predict predator–prey interactions. This model fits data remarkably well (Portalier et al., 2019). The model provides a detailed mechanism for predation, where predators have to move around for searching, capturing and handling their prey. All these aspects depend on the body masses of both the predator and its prey. The parameters of the functional response can be immediately computed from the biomechanical model. Hence, this model provides a novel method to parameterize a functional response based on individual traits, and on using mechanical laws. According to the biomechanical model assumptions, it is well suited for pelagic organisms.

Main framework

This model uses body size and physical features of the medium to predict predator–prey interactions. Hence, the model requires the body masses of both the predator and its prey. The physical parameters are acceleration due to gravity, body density, medium density, and medium viscosity. Then, the model computes all the necessary information to predict feasible predator-prey interactions.

Predation is broken down into three successive sequences: a predator needs to search, capture, and then handle its prey. Each predation sequence leads to a time expenditure and requires motion. Following the idea developed by Bejan and Marden (2006), motion is modelled as an oscillatory process that is decomposed into three sequences. First, an organismal stroke leads to a thrust that propels the body upwards (following Archimedes' force, but facing gravity and drag (D) due to density and viscosity) and forwards (facing drag). It is possible to numerically derive vertical speed from simple mechanical laws:

$$\dot{v} = \frac{F_{Mv}}{M_b} + \frac{g\rho V_b}{M_b} - g - D(v, M_b, \rho_m, \mu) \qquad (1)$$

152   where v is instantaneous vertical speed, F_{Mv} is thrust vertical force, M_b is body mass, g is

153   acceleration due to gravity, V_b is body volume, ρ is medium density, D is drag that varies with

154   speed, body mass, density, and medium viscosity (μ). Second, when stroke ends, the body

155   continues its ascending movement by inertia until its stops.

$$\dot{v} = \frac{g\rho V_b}{M_b} - g - D(v, M_b, \rho_m, \mu) \qquad (2)$$

156   Third, the body returns by inertia to its original vertical position.

$$\dot{v} = -\frac{g\rho V_b}{M_b} + g - D(v, M_b, \rho_m, \mu) \qquad (3)$$

157   During this vertical oscillation, the body moves forward compared to its original

158   horizontal position over a distance that depends on the forward component of thrust. The

159   instantaneous horizontal speed can be derived using a method similar to vertical speed, but it

160   considers only thrust and drag (see supplementary material for more details). Then, another

161   sequence begins. The model computes the thrust force needed to propel the body (which is

162   constrained by body size), the horizontal distance covered, the speed and the associated energetic

163   cost that maximizes the probability to capture a prey, and the net energy gain from its

164   consumption. Predicted speeds fit data well (Fig 1). Both predator and prey follow the same

165   rules, with the difference that the prey only maximizes its probability to escape predation.

166   Predation on a given prey requires first its encounter, followed by capture and finally

167   handling. Encounter rate is determined by the speeds of the predator and prey calculated in the

168   model (see above), and then used in a formula according to (Rothschild and Osborn, (1988). The

169   relative speed between the predator and the prey calculated at the time of capture also determines

8

170   the probability of capture (and therefore the total time for searching a prey that leads to a

171   successful capture), and time for capture. Search time (t_s) represents the time needed by a

172   predator to contact a prey that leads to a successful capture (e.g., if the capture probability is 0.5,

173   then the predator needs to contact a prey twice on average to successfully capture it). Capture

174   time (t_c) is the time needed to move towards a prey and seize it. Last, handling time (t_h) is the

175   time needed to consume and digest the prey (handling time is the only component in the model of

176   the functional response that is independent of physical factors). The functional response ($f(N)$) is

177   defined as the inverse of the time needed for searching, capturing and handling one unit of prey

178   of abundance N. The function may be written as follows (see supplementary material)

$$f(N) = \frac{N\beta P_c}{1 + N\beta P_c(t_c + t_h)} \tag{4}$$

179   βP_c represents the attack rate, where β is the encounter rate (constrained by predator and prey

180   speeds), and P_c is the capture probability. Capture time and handling time are taken into account

181   instead of handling time only. Under this form, one can recognize a modified version of Holling's

182   disk equation (1961).

183   Given the assumptions made on the encounter rate (see Supplementary Material), the

184   functional response behaves as a type-II response. All parameter values change according to both

185   predator and prey sizes, while attack rate, capture probability and capture time also vary with

186   mechanical features of the medium.

187   **Validation of the model**

188   Data were collected in order to test predictions from the model. Most data come from two meta-

189   analyses (Hirt et al., 2017; Li et al., 2018), as well as our own literature search (cite here if only a

190   couple of papers, or add a table with references in the supplementary material). To be pertinent,

191 data have to mention predator and prey sizes explicitly. Most data are individual-based, which

192 means that two individuals from the same species but with different sizes are treated separately.

193   Predicted attack rate, capture probability and handling time were compared to real data

194 coming from aquatic systems (Fig. 2). It appears that the model fits the data quite well for attack

195 rate (except for very small organisms, but there is also a limited amount of data) and capture

196 probability. Linking mechanical features from the medium and body size allows a good estimate

197 of attack rate and capture probability for pelagic predators. However, handling time is usually

198 underestimated for small predators, while the model is more accurate for larger predators. This

199 discrepancy for small predators opens the door to many hypotheses that remain to be tested. Note

200 that this parameter is not dependent on mechanical features of the medium, but is determined

201 only by allometric laws. Thus, the results suggest that the relationship between predator size, prey

202 size and handling time is driven by a more complex set of allometric laws that differ between

203 small and large predators (Emerson et al., 1994), or that other factors increase handling time for

204 small predators. Some studies also suggested that handling time may not be static for a given

205 predator, but vary with prey abundance (Okuyama, 2010). These are examples of hypotheses that

206 can be inferred from the analysis of such a model.

207 **Conclusions and future directions**

208   The model proposed here uses the mechanical properties of the medium to develop a

209 mechanistic approach to the functional response. However, it considers only a limited set of

210 physical factors. The model could be improved in several ways. Future studies could include

211 more physical factors such as temperature, which affects the physical properties of the medium

212 (Larsen and Riisgård, 2009), and organisms' metabolism (Brown et al., 2004). They could also

213 consider factors that affect prey detection such as light and chemical cues. These factors diffuse

214 differently in air and water, the perception ability of predators seems to be related to size

215 (Martens et al., 2015). This novel framework is promising because it provides easy ways to

216 validate or falsify hypotheses. Hence, any discrepancy between predictions and real data points

217 immediately towards an error in the model, or it means that important mechanisms are missing

218 (as shown for handling time in our case study). It can also suggest novel hypotheses to be

219 empirically or theoretically tested.

220   In our model, processes based on mechanical factors (i.e., speed, attack rate, capture

221 probability) fit data well. Handling time shows a lower goodness of fit, and it is the only one that

222 does not include any physical factors. A better mechanism for handling is thus needed. Ingestion

223 has received some attention in the existing literature, especially for aquatic organisms (Holzman

224 et al., 2012). Mechanisms driving digestion have also received some attention. For example, there

225 are models of gut motility according to prey size and gut volume (Salvanes et al., 1995), although

226 they usually do not include physical factors from the medium that may affect the process (e.g.,

227 temperature, pressure). However, both ingestion and digestion models might be difficult to

228 generalize to a large variety of species (and sizes). Moreover, other aspects of handling time are

229 likely to play a role. For instance, prey subjugation before ingestion is an essential aspect.

230 Unfortunately, studies on this topic seem to focus either on dangerous (e.g., poisonous) prey

231 (Mukherjee and Heithaus, 2013), or on specific species (Schatz et al., 1997), which makes them

232 difficult to generalize. Last, predator satiation or hunger remains a fundamental aspect of predator

233 activity (Jeschke et al., 2002). While it has been included in several studies, its underpinning

234 processes remain to be modelled. Therefore, a generic mechanical description of handling that

235 would cover its different components and be valid across a wide range of sizes would represent a

236 significant improvement.

237   More generally, the strength of this kind of approach is to derive patterns at the

238   community level from measures done at the individual or species level. Thus, the functional

239   response is an emerging property of the system. One could even go further by including other

240   aspects associated to predation such as behavioral features (e.g., predator avoidance, interference

241   between predators, social aspects) that were already considered by Holling (1966). This approach

242   opens up a promising avenue for new studies that would merge the biological part and the

243   physical part of the medium.

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Contribution of authors

247   S.P. led the writing of the manuscript, implemented the model, gathered data, and performed

248   simulations and analysis. M.C., G.F. and M.L. provided conceptual advices and guidance. All

249   authors discussed the results and contributed equally to earlier drafts.

Data accessibility

251   Data and the MATLAB code used to implement the model will be stored in a public depository

252   should the manuscript be accepted. During the review process, data and code will be made

253   available in a temporary archive on GitHub:

254   https://github.com/sportalier/Code_Data_Frontiers_In_Ecology_And_Evolution.git.

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391

392 **Figure 1**: Species-specific speed according to body size for organisms moving in aquatic

393 systems. Speed increases with body size since overall muscular power generating thrust increases

394 with size. Despite variation among species, the predicted speed fits data well (data from (Hirt et

395 al., 2017)). However, the model does not predict the relative reduction of speed for very large

396 animals since it does not include any specific mechanism to do so.

397

398 **Figure 2**: Predator attack rate **(A)**, capture probability **(B)** and handling time **(C)** according to

399 predator mass in aquatic systems. The model fits the data quite well for attack rate (except for

400 very small organisms) and capture probability. However, data show some variability. Predictions

401 for handling time are more accurate for relatively large predators than for smaller predators. This

402 suggests that more investigations are needed in order to understand how mechanical factors

403 constrain handling time for predators according to predator and prey sizes.
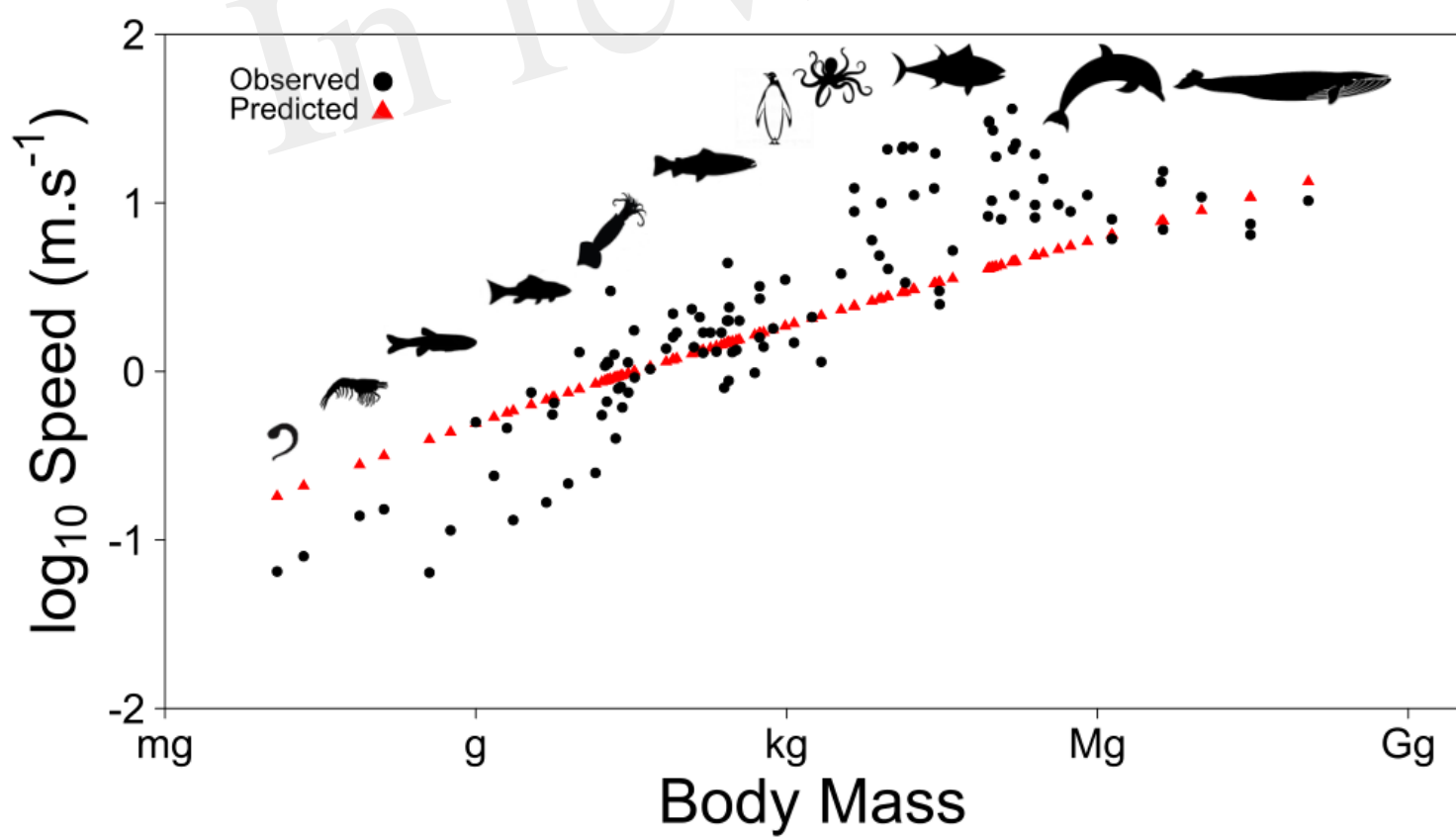
Figure 1.TIFF

Figure 2.TIFF