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

# **Abstract**

First derivations of the functional response were mechanistic, but in practice, the subsequent uses of these first mechanistically-derived functions were mostly phenomenological and, to a large degree unsatisfactory. However, a better understanding of mechanisms underpinning functional response would lead to novel insights on predator-prey relationships within natural systems. We propose to return to the mechanistic approach, and we try to push it by including an explicit consideration of the movement of the organisms involved, and hence of mechanics. Living organisms are constrained by the physical properties of the surrounding medium. Hence, ability of moving is an essential aspect of most predator-prey interactions, and motion is affected by physical properties such as density or viscosity. A predator has to move to search for a prey, then to capture this prey. Search and capture efficiencies are key elements of attack rate. Physical properties of the medium, in relation with body size, constrain predator and prey ability to move, thus affecting functional response. Considering mechanical effects from the medium grounds the functional response within its physical, local environment, and makes its parameterisation dependent on measurable morphological and physical traits of organisms. As an example of this kind of approach, we provide a model that derives classical parameters of a functional response (i.e., attack rate and handling time) from body size and physical factors. We use a recently published biomechanical model, and compute parameter values for a functional response. The novelty of this approach is that parameters are not estimated from observational data. The model only needs body sizes and physical properties of the medium, which can be easily measured.

Several ways for potential improvement are discussed. Further studies may include more physical factors such as temperature that affects physical properties and/or organism metabolism, or light that may be of importance for visual predators. This approach also provides easy ways to validate of falsify hypothesis. Hence, discrepancies between predictions and real data point immediately towards an error in the modelling, or means that important mechanisms are missing. Using this approach, functional response becomes an emerging property of the system. It opens a promising avenue for new approaches that would merge the biological part and the physical part of the medium. The strength of this kind of approach is to derive patterns at the community level from measures done at the individual or species level.

# **Introduction**

The study of the consumption rate of prey by a given predator (i.e., the functional response) began several decades ago (Gause, 1934; Gause et al., 1936). Quickly, the need of a theoretical framework emerged, and several mechanistic approaches were proposed (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 encounter and capture prey) and handling time (the time needed by the predator to subdue, ingest and digest the captured prey, and during which the predator cannot attack another prey). These parameters can be measured independently, and they give information about factors that constrain predation on a given prey, which is the strength of this mechanistic approach.

However, since Holling proposed the type-I, II and III models of functional responses, the subsequent uses of these first mechanistically-derived functions have been, in practice, mostly phenomenological and, to a large degree unsatisfactory. Hence, many studies investigating functional response use a type-II or a type-III model, or any subsequently derived model (e.g., Rogers (1972)) as an *a priori* framework from which authors derive the values of attack rate and handling time from the data (e.g., Andresen and van der Meer, 2010; Farhadi et al., 2010; Papanikolaou et al., 2011)). These approaches give valuable information on the studied systems, and they allow for hypothesis testing: for example, the effects of temperature (Archer et al., 2019) or predator satiation (Li et al., 2018) on functional response. However, they do not provide a real explanation on the mechanisms constraining attack rate, handling time, and therefore the functional response. Moreover, these studies are mostly carried out in laboratory, where many external factors do not apply (Abrams, 1982).

Coming back to the mechanistic roots of the functional response approach, several studies investigated the role played by factors known to affect the functional response. These models emphasized different features of predator-prey relationships, such as feeding saturation (DeAngelis et al., 1975)⁠, interference between predators (Beddington, 1975)⁠, or interaction between predators (Wasserman et al., 2016)⁠. Among them, the body sizes of predator and prey is known to strongly affect the functional response (Aljetlawi et al., 2004; Vucic-Pestic et al., 2010)⁠. It appears that body size is a good predictor of trophic position (Williams et al., 2010)⁠ and affects the overall dynamics of the interaction (Yodzis and Innes, 1992).

However, the surrounding physical medium remain absent or at least implicit in most models, despite its ubiquity in real ecosystems. Although in his pioneer work Tansley (1935) stated that organisms should not be separated from their “special environment, with which they form one physical system”, the role played by the physical medium in constraining the functional response remains largely unexplored. Including physical features into predator-prey models would lead to novel insights about species interactions.

# **Physical features of the medium and size-related constraints**

Previous studies that considered the surrounding medium usually focused on specific aspects of predation or on specific taxa (Domenici et al., 2011)⁠, or investigated specific aspect of the medium such as dimensionality (Pawar et al., 2012)⁠ or complexity (Barrios-O’Neill et al., 2016)⁠. However, the role played by the surrounding medium acting at the individual level on predator-prey relationship, driving the functional response, remains to be explored.

Hence, living organisms are constrained by the physical properties of the surrounding medium (Denny, 1993; Denny, 2016; Vogel, 1996)⁠. These properties affect the way organisms move and/or interact with each other in different ways. For example, in aquatic systems, turbidity is an essential factor that constrains predator or prey that rely on visual cues to detect each others (Martens et al., 2015). Another example is turbulence that controls many planktonic organisms suspension within the water column (Rodríguez et al., 2001), and affects contact rate between predators and prey (Kiørboe and Saiz, 1995).

An important aspect is the role played by mechanical factors (i.e., gravity, density and viscosity) in constraining motion. Aquatic organisms do not experience the effects of gravity as terrestrial organisms usually do because medium density is much higher in water than in air, which creates buoyancy. Since predation usually implies motion, these factors create mechanical constraints acting on predators. These mechanical factors are ubiquitous and affect small predators (Kiørboe and Saiz, 1995), as well as large predators (Howland, 1974; Domenici et al., 2007)⁠. Actually, these effects are usually size-dependent: especially, the effects of medium viscosity and density on species motion through drag. Hence, motion of planktonic organisms has very different features than motion of larger organisms. Metrics such as Reynolds number are commonly used to discriminate between organisms that experience huge drag (low Reynolds number) and those that experience more inertia (high Reynolds number). These features affect the species according to their size and shape (Koehl and Strickier, 1981; Koehl, 1996). Hence, incorporating mechanical constraints into models would lead to a better understanding of the size-based relationship between predators and prey, and even of the size-structure of food webs.

Models incorporating physical (including mechanical) factors into predation model would merges size-related biological and mechanical constraints within classical predator-prey systems. Parameters in the model would be (mostly) related to predator and prey sizes, a trait that is commonly measured, which makes conclusions from the models easily testable. The real novelty of this kind of approach is the fact that the parameters of the functional response are not measured at the community level, but are derived from the individual (or species) level. Hence, classical parameters such as attack rate and handling time become emerging properties of the model. Another other strength of this approach is to allow for hypothesis testing, since discrepancies between predicted and observed patterns would point out to incomplete or erroneous hypothesis.

In order to illustrate this novel approach, we propose to include some of these mechanical factors related to body size into a theoretical model that predicts the functional response for a given predator and 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 to 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 for searching, capturing and handling their prey. All these aspects depending on the relative body mass ratio between a predator and its prey. Some elements computed by the biomechanical model can be used to parameterize a functional response. Hence, this model provides a novel method to parameterize a functional response based on individual traits, and 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 to prey interactions. Hence, the model requires 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 necessary information to predict feasible predator-prey interactions.

Predation is broken up into three successive sequences: a predator needs to search, capture and then handle its prey. Each predation sequence leads to time expenditures. Thus, predation on a given prey requires time for searching, time for capturing and time for handling this prey. Each predatory activity implies motion, and motion is constrained by physical factors (mentioned above). The functional response (*f(N)*) is defined as the inverse of the time needed for searching, capturing and handling one unit of prey of abundance *N*. The function may be written as follows (see supplementary material)

*βPc* represents attack rate, where *β* is encounter rate (constrained by search time), and *Pc* is capture probability. Capture time (*tc*) and handling time (*th*) are taken into account instead of handling time only. Under this form, one can recognize a modified version of Holling's disk equation (1961).

Given the assumptions made on the encounter rate (see Supplementary Material), the functional response behaves as a type-II one. All parameter values change according to both predator and prey sizes, while attack rate and capture time also vary with mechanical features of the medium.

## **Validation of the model**

Data were collected in order to test predictions from the model. Most data comes from meta-analysis⁠. To be pertinent, data has to mention predator and prey sizes explicitly. Most data is individual-based, which means that two individuals from the same species, but with different sizes would be treated separately.

Attack rate and handling time were compared to real data coming from aquatic systems (Fig. 1). It appears that the model fits data quite well for attack rate. Linking mechanical features from the medium and body size allows a good estimate of attack rate for pelagic predators. However, handling time is usually underestimated for small predators, while the model is more accurate for larger predators. This discrepancy for small predators opens the door to many hypotheses that remain to be tested. Hence, this parameter is not dependent on mechanical features of the medium, but is driven only by allometric laws. Thus, the results suggest that the relationship between predator size, prey size and handling time is not only driven by an allometric law that is valid across a wide range of sizes. It is possible that the slope of this allometry function is different between small and large predators (Emerson et al., 1994), or that other factors increase handling time for small predators. Some studies suggested that handling time might not be static for a given predator, but can vary with prey abundance (Okuyama, 2010). These are examples of hypothesis that can be inferred by the analysis of such a model.

# **Conclusion and future directions**

The proposed model uses medium mechanical properties in a mechanistic approach. It considers only some physical factors. It can be improved in several ways. Further studies may include more physical factors such as temperature that affects physical properties (Larsen and Riisgård, 2009) and organism metabolism (Brown et al., 2004). One can consider factors that affect detection such as light or chemical cues. These factors diffuse differently in air and water, and perception ability by predators seems to be related to size (Martens et al., 2015). This novel framework is promising because it provides easy ways to validate of falsify hypothesis. Hence, any discrepancy between predictions and real data points immediately towards an error in the model, or means that important mechanisms are missing (as shown for handling time in the case study). It can also suggest novel hypothesis to be empirically or theoretically tested.

The strength of this kind of approach is to derive patterns at the community level from measures done at the individual or species level. Thus, functional response becomes an emerging property of the system. One may go even further by including other aspects associated to predation such as behavioral features (e.g., predator avoidance, interference between predators, social aspects) that were already considered by Holling (1966). This approach opens a promising avenue for new studies that would merge the biological part and the physical part of the medium.

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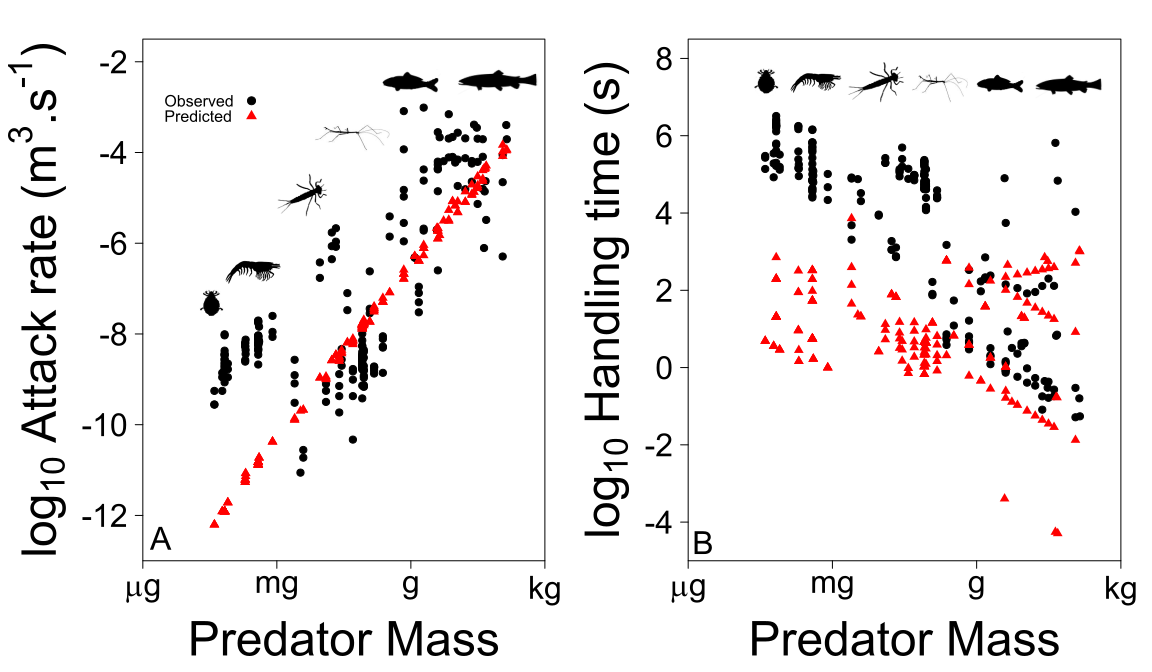
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**Figure 1**: Predator attack rate (A) and handling time (B) according to predator mass in aquatic systems. The model fits data quite well for attack rate, although data shows variance. Predictions for handling time are more accurate for relatively large predators than for smaller predators. This suggests that more investigations are needed in order to understand which factors constrain handling time for smaller predators.