**Predator and prey encounter rates and local prey densities are modulated by prey behavior**

Matthew S. Woodstock1,\*, Jean Paul Mattern2, Gregory L. Britten1

1Woods Hole Oceanographic Institution

2Paul’s Affiliation

\*Corresponding Author: Matthew S. Woodstock (matthew.woodstock@whoi.edu)

# Abstract

The predation efficiency of an animal is a function of the surrounding prey density with limitations caused by handling time and clearance rates. Typical methods to estimate prey density are coarse evaluations of preys within a given area, but little consideration has been given to the distance between predator and prey, or the influence of patchiness on potential predator-prey encounters. Individual-based modeling is becoming more tenable as computational power increases, meaning that refined consumption rate estimates are possible for more complex modeling approaches. We developed a three-dimensional, two-species model that includes varying predator and prey swimming velocities, visual abilities, and a range of prey abundances to evaluate the effect on encounter rates, functional response curves, and estimated consumption rates. Encounter rates were a function of prey abundance, following a Type II ecological functional response curve (logarithmic curve), and the steepness of this relationship was influenced by the relative swimming velocity between predator and prey, and partially by the prey’s visual ability. Although each predator could perceive 50% of the modelled prey field, the number of preys within the predator visual range was almost always less than 50% in all simulations, indicating that patchiness is a function of both prey behavior and the absence of preys in an area after they are consumed. The emergent consumption rate estimates from locally calculated prey densities were less than global prey density calculations, and local prey densities resulted in variance scaling to the variability in local prey densities among all predators. Local prey densities are a necessary calculation for individual-based predator/prey models because they provide consumption rate estimates based on a refined estimate of the surrounding prey field with considerations to behavioral impacts on predator/prey dynamics.

**Keywords:** Predator/prey dynamics, Individual-based modeling, Food webs, Functional Responses, Theoretical Modeling

# Introduction

The foraging efficiency of a predator is a function of the surrounding prey density, prey handling time, and satiation of the predator, which influence encounter rates (RECENT PREDATOR/PREY DYNAMICS). Changes to these parameters result in non-linear adjustments to a predator's estimated consumption rate, termed ecological functional response curves (Holling 1965). Many food-web models utilize these relationships and simulated changes in predator and prey populations to project the consumptive effects of predator species to specific prey populations and holistic predation impacts (ECOSYSTEM MODELING SOURCES). Other models create functional response curves as an emergent property of the simulation (SOURCES). Since ecosystem models must limit their taxonomic and spatiotemporal resolutions to reduce overall model complexity and resulting noise (BETH FULTON SOURCE), currently used software is not capable of incorporating individual animal behaviors into functional response curve estimates. Novel food-web modeling approaches are being developed with faster programming speeds (e.g., Julia Programming Language; SOURCES), creating the possibility for individual-based modeling (PLANKTONINDIVIDUALS SOURCE OR OTHERS). Individual-based models may still require ecological functional response curves as inputs,

Marine populations are often organized as heterogenous patches (SOURCES). Conventional food-web models consider spatiotemporal scales coarser to the scale of the occuring biological processes (SOURCES). This scale mismatch results in a poor ability to simulate patchiness in aquatic environments, and may create erroneous prey density calculations when considering the ecosystem from the perception of each individual. Prey density calculations involve aggregating the abundance (or biomass) of potential preys and dividing by the total area of the assumed target area, generally a grid cell (SOURCES). However, if the predator cannot percieve the entire environment through sensory limitations (e.g., visual ability is less than the model grid), the calculation will be considering localities the predator cannot forage. A more accurate estimate may be to calculate the number of preys in the perceivable area of each predator and calculate individual predator foragaing efficiencies, which could then be aggregated to the species-level with quantified variance (Figure 2).

A screenshot of a video game

Description automatically generated

Figure . A schematic of the challenges associated with calculating prey density in an individual-based framework as two predators (orange) have different prey (blue) densities depending on if that density is calculated from the global scale (full grid cell) or localized scale (the visual range of the predator; red). The perception range could apply to all sensory functions.

Many animals rely on visual cues to perceive their environment, and the visual acuity of animals varies widely. In the oceanic zone, larger predators (e.g., tunas, swordfishes) are capable of seeing much further distances than their preys because of the presence of an aphakic gap (fluid-filled gap between the inner and outer eye lense), indicating there is an evolutionary advantage to seeing further in habitats devoid of physical structure (REF). This visual acuity is coupled with streamlined body shapes with additional features designed to reduce drag (e.g., keels on tuna) (SOURCES). Oceanic models may consider the magnitude of these differences as a factor in predation ability, but few modeling frameworks explicitly incorporate the animal's visual acuity as a factor in an animals decision making.

Interest into developing individual-based models have been on the rise as there is an increase in computational power and understanding that marine food webs vary over space and time (SOURCE). Additionally, there is strong logic behind incorporating species’ traits with regime-shift theory (Weisberg et al. 2023), which will require refined mechanistic modeling approaches Individual-based models have primarily been used for single-species investigations, but there is interest in developing more holistic, ecosystem-scale models the incorporate species-specific traits and animal behaviors. Time-dynamic food-web models that include individual animal decisions require a mechanistic understanding of how individual animal decisions may influence a predator’s foraging efficiency.

In this study, we developed a three-dimensional, two-species model to examine changes in the encounter frequency of predators and preys among various prey abundances, swimming velocities, and visual ranges. Functional response curves emerged as the relationship between encounter frequency in the simulation and a progression of examined prey abundances. The effect of prey swimming velocities and visual ranges were tested and described in relation to the predator swimming velocity and visual range. The prey density was calculated as both a grid-based density and individual-based density and consumption rate estimates were derived.

# Methods

## Model Structure

The encounter rates of predator and prey species were examined using a modified version of PlanktonIndividuals.jl (Wu et al. 2022) that allowed for direct and active animal movement, and limitations to an animal’s perception of its environment (i.e., visual range, hereafter). The theoretical model domain was a 10 meters x 10 meters x 10 meters cube (1,000 cubic meters in volume) with no structural habitat, best simulating a pelagic environment. Only active movement (i.e., swimming) was considered when moving individuals and no spatial restrictions were placed on animal movement (i.e., the entire habitat was considered equally suitable). Both the predator and prey species were provided a scalar movement velocity vector (Table 1).

Table . The state variables used during the simulation and the calculation of consumption perceivable prey density

|  |  |  |
| --- | --- | --- |
| **Parameter** | **Value** | **Units** |
| *Simulation Parameters* |  |  |
| Predator Abundance | 50 | Individuals |
| Prey Abundance | 25–900 | Individuals |
| Predator Swim Speed | 0.01 | m s-1 |
| Prey Swim Speed | 0.0001–1 | m s-1 |
| Predator Visual Range | 4.92 | m |
| Prey Visual Range | 0–62.04 | m |
| Simulation Length | 300 | minutes |
| Handling Time | 8 | minutes |
| *Consumption Parameters* |  |  |
| Clearance Rate | 0.01 | m3 ind-1 s-1 |
| Prey Weight | 5 | g |
| Prey Energy Density | 5,000 | Joules |
| Predator Capture Success | 0.7 | Dimensionless |

## Simulations

The predator-prey encounter rates were examined as a function of prey abundance (25–900 individuals at varying intervals), prey velocity (0.0001–1 m s-1), and prey visual field (0–62.04 m radius; Table 1). Predator velocity (0.01 m s-1), predator visual field (4.92 m radius; i.e., half of the model domain), predator abundance (n = 50 individuals), and predator handling time (8 minutes) were the same in each simulation. Boundary effects (i.e., preys trapped in model domain corners by predators) were removed by allowing both predators and preys to “jump” from one end of the grid to another, creating an endless domain. The domain size, movement velocities, and visual fields were chosen to provide a relative representation of two hypothetical species. Since these parameters will vary with species’ morphology and visual capabilities, these parameters do not necessary represent one particular predator-prey interaction, but instead are designed to explore how encounter rates vary in relative relation to each other. Prey abundances remained constant throughout each simulation (i.e., no fluctuation prey abundance) and consumed preys were respawned at random coordinates. Random spawning potentially created encounters if a prey was spawned in a suboptimal location near a predator, so ten iterations were conducted for each scenario. All predators and preys moved at each time step. The predators attempted to move towards the closest prey and the prey attempted to move towards the optimal location to avoid all predators within their visual range (i.e., furthest location from all predators). If there were no preys within the predator’s visual range or no predators within the prey’s visual range, the individual moved at a random vector at a distance consistent with their swimming velocity. When predators reached preys, consumption occurred and an eight-minute handling time period was applied to that predator. The simulation operated at a one-minute scale and continued for 300 minutes. The encounter rate (N encounters timestep-1) was calculated for each simulation and comparisons were made among prey velocities, visual fields, and abundances.

Two prey densities (*n*) were calculated during each simulation, a global prey density (prey abundance / volume of model domain) and local prey density (n perceivable preys / volume of perceivable area). Within simulations, the global prey density was the same for each predator because prey abundance and the size of the model domain were constant throughout the simulation. However, each predator could experience a different local prey density and this value could vary throughout the simulation for each individual. During the last time step of each simulation, the number of preys within each predator's perceivable area was recorded. The last timestep reflected the combined effects of each preceding timestep's animal movements and had the most refined estimate of the preys surrounding each predator. Global and local prey densities were converted to consumption (*C*; Joules) according to an assumed Type II ecological functional response curve (Equation 1; (Langbehn et al. 2019)).

(1)

where clearance rate (*c*; 0.01 m3 min-1 ind-1) and handing time (*h*; 8 minutes) parameters estimate the encounter rate used in the equation. A predator success coefficient (*pc*; 0.7), prey weight (*w*; 5g), and prey energy density (*d*; 5,000J) convert the estimated encounter rate to the possible biomass consumed during that time step. Although the initial model assumed predator’s were always successful, a value of 0.7 was considered more realistic and was applied to both grid-based and individual-based densities. The chosen values represent those that may be realistic for this model domain, but could be any, as they would scale equally for both global and local prey density-consumption calculations.

# Results

## Encounter Rates

The encounter rates experienced between predator and prey were a function of prey density and followed a Type II ecological functional response curve (Figure 2). Encounter rates were smallest at the smallest prey abundance (n = 25 preys), ranging from 5 × 10-3 (± 3 × 10-3) encounters timestep-1 at the fastest simulated prey velocity to 0.44 (±0.02) encounters timestep-1 at the slowest simulated prey velocity. Encounter rates were greater when preys were blind (0 m prey visual range) compared to simulations of the same prey velocity and abundance (Figure 2), indicating that the ability for the prey to make optimal movement choices influences ecological functional response curves. When the prey had a visual range greater than 0 m, preys that had an equivalent swimming velocity to the predator always had visual encounter rates less than 0.11 encounters timestep-1, regardless of prey abundance. Beyond the 3 m visual range, the prey’s visual acuity had little effect on the predator/prey encounter rate (Figure 2). Prey density and prey velocity have the greatest effect on the encounter rates between predator and prey in a fixed-space ecosystem, while a prey's ability to perceive the environment has limited influence on encounter rates.

A group of graphs showing different colors

Description automatically generated with medium confidence

Figure 2. The effects of prey velocity (colors) and visual range (panels) on functional response curves. Visual range panels correspond to the distance the prey can perceive and was calculated as the radius of an assigned visual field volume. The predator velocity (0.01 m s-1), visual range (49 m; half of the model domain), and abundance (n = 100 individuals) were the same in each simulation.

Predator/prey encounter rates have a logarithmic relationship with the relative swimming velocities of predator and prey. When predators are 100x faster than preys, encounter rates have a maximum of 2.6 (± 0.06) encounters timestep-1, whereas when preys are 10x faster than predators encounter rates have a maximum of 0.3 (± 0.04) encounters timestep-1 (Figure 3). The encounter rates when preys are 10x faster than the predator are similar to simulations where the preys have the same swimming velocity to the predator, when preys are capable of seeing predators. An inflection point occurs in this relationship between equivalent predator/prey swimming velocities and predator velocities greater than 10x the prey (Figure 3). At low predator/prey swim speed ratios, prey abundance does not influence the number of encounter rates. However, at high predator/prey swimming speed ratios, the highest prey abundances also influence prey encounter rates. Encounter rates are influenced by the prey’s ability to avoid predation, and this effect is greatest in between equivalent predator/prey swimming velocities and when predators are one order of magnitude faster than preys.

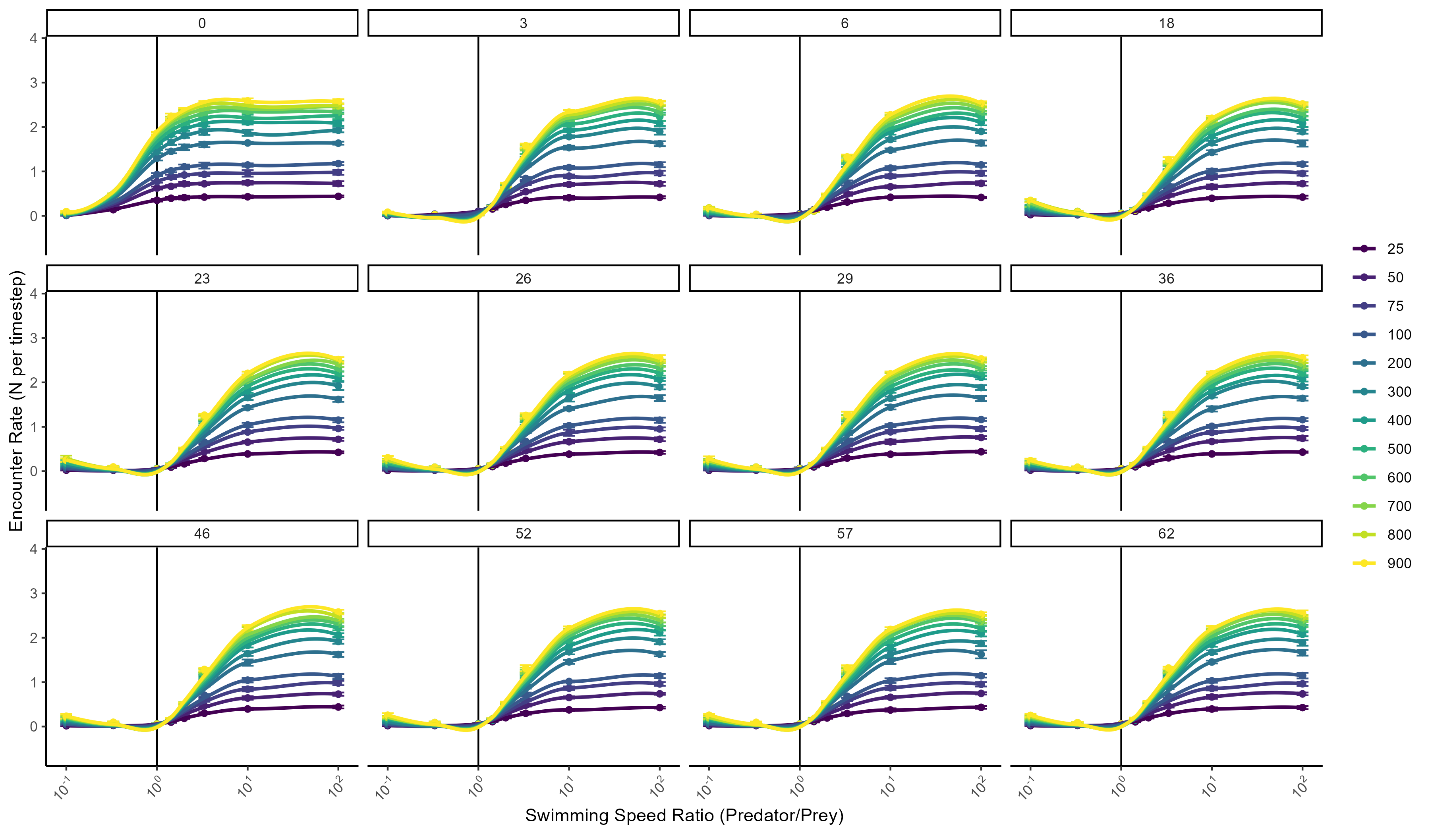


Figure . The relationship between predator-prey encounter rates and predator-prey relative swimming velocities (log-transformed). Prey abundances are represented as colors and prey visual range (visual distance; m) are represented as facets. Predator velocity (0.01 m s-1; vertical black line), abundance (n = 100 individuals), and visual range (49 m; half of model domain) are constant in each simulation.

## Prey Density and Consumption

The number of perceivable preys per predator was greatest at high prey densities than at low prey densities for all prey swimming velocity and prey visual range combinations (Figure 4A; Supplemental Figures XX-XX). In a homogenous environment where the predator can perceive 50% of the volume, it would expected that the predator could perceive 50% of all available preys. However, the proportion of all preys within the perceivable area peaked between 20% and 40% per predator among all of the prey abundance scenarios, independent of overall prey abundance (Figure 4B). There is a positive relationship between prey density and the variance in the number of perceivable preys per predator (Figure 4C). Since local prey densities were almost always less than 50% of the total available preys, the estimated encounter and consumption rates that emerge from these prey densities, are anticipated to be less than those derived from a global prey density calculation.

A screenshot of a graph

Description automatically generated

Figure . A) Density ridgeplots of the number of preys within each predator's perceivable area. These results only reflect the scenarios where prey velocity was equivalent to the predator and visual range was 46 m. B) The proportion of available preys within the model domain that were within the perceivable range of the predator. C) The relationship between the standard deviation of the perceivable prey distribution and modelled prey abundance separated by prey swimming velocity (colors) and prey visual range (facets). Only four select prey visual distances are represented. All other relationships are in Supplemental Figures XX-XX.

Following a Type II ecological functional response curve, the derived consumption rates from local density estimates were nearly always lower than the global density estimates. The global density-derived consumption rates produced functional response curves that were the same for all pairings, since the global estimate was simply the number of preys divided by the volume of the model domain (i.e., two constants). This global estimate ranged from XX–XX J timestep-1. The local estimates had minimum and maximum values of XX (± XX) and XX (± XX) J timestep-1, respectively. The 95% confidence intervals of consumption from the local densities were similar, regardless of prey swimming velocity and visual range. The variance in these confidence intervals ranges from XX (CONDITION) to XX (CONDITION) and is a reflection of the differences in individual prey densities, the non-constant only variable in the given functional response curve equation. This calculation only considers that the preys are within the perceivable area of the predator, and has a constant predation success (70% for all calculations). However, even without adjusting for individual qualities that may influence predator predation success (e.g., predator/prey body size, prey behavior, predator body condition, predator motivation to feed), the estimated consumption rates derived from local prey densities are lower than global density estimates, a difference that would accumulate in more complex models.

A screenshot of a graph

Description automatically generated

Figure . The consumption rates derived as a function of prey density encounter rates as a function of prey abundance. Relationships are divided among all tested swimming velocities (columns) and visual acuities (rows). Both grid-based response curves (red line) and individual-based response curves (black ribbon) are shown.

# Discussion

## Encounter Rates

The inclusion of prey behavior in the form of varying swimming velocities and visual ranges through an optimal movement algorithm advances our understanding of functional response curves from the individual predator perspective. Similar to the population scale, predator-prey encounter rates are primarily influenced by prey density and led to the emergence of a Type II ecological functional curve in all simulations where the predator was faster than the prey. Open-ocean ecosystems are often believed to be organized in size-selective feeding patterns (Menard et al. 2006, Van Den Hoff et al. 2018). Although there is evidence for taxon-specific feeding within prey communities (Spitz et al. 2010, Drazen and Sutton 2017), morphological constraints mean mobile predators generally feed upon preys smaller than themselves. It is most likely that open-ocean encounter rates can be predicted using Type II ecological functional response curves. However, the inflection points and asymptotes of these curves were influenced by prey behavior at predator-prey swimming velocities within an order of magnitude. The swimming velocities of XX and XX, a common predator-prey interaction was XX m s-1 (SOURCE) and XX m-1(SOURCE). The encounter rates of species that have swimming velocity differences less than one order of magnitude are likely influenced by prey behavior, which requires an individual-based framework to explicitly model.

## Nonlinear Modulation

Within one order of magnitude swimming velocity, prey visual capacity influenced the functional response curve. A visual distance of 18 meters (2.5% of the model volume), compared to 49 meters for the predator, allowed for preys that was 1/3 of the swimming capabilities as the predator to decrease encounter rates by *c.* 50%. Increasing the visual range beyond this amount did not have a further impact on the functional response curve. INCLUDE SOURCE ABOUT THE EVOLUTIONARY RESTRAINTS OF BETTER VISION. Hypothetically, the optimal foraging procedure also increased the foraging time of each successful predation event, as predators would have to work harder to catch preys. In a more complex simulation (e.g., three or more species, multiple predator or prey species, considerations to environmental and distance-based energetic constraints) prey avoidance could have a greater influence on encounter rates as individual predators would have to adjust their optimal foraging strategy at each time step.

More advanced modeling efforts could integrate species-specific traits that influence swimming velocities (e.g., comparative morphologies, predation strategies).

## Prey Density and Consumption

* Prey fields in the open ocean are not homogenously distributed (SOURCES).

- Individual-based assessments should consider that predator and prey behaviors will influence functional response curves.

- Describe real-life limitations that could confound this result

3) Although the predation procedure in this model was simple and predators were constantly motivated without limitations to their energetic expenditure, faster preys could effectively avoid predation by placing themselves further away from the predator than another prey. There are mechanistic problems with testing this hypothesis, as open-ocean predator-prey dynamics are generally size-structured (Menard 2006), but the differences observed suggests that the optimal avoidance algorithm was effective, so long as the preys were physically able to outpace the predator.

4) Predator swarming behavior is a useful tactic for many large marine predators to increase predation efficiency by trapping preys between multiple predators that are attacking from multiple directions (SOURCES). This was not explicitly incorporated into this model algorithm. Instead, all predator individuals had an independent, but shared motivation (i.e., catching the nearest prey). Encounter rates should have been nearly absent in scenarios with a prey swimming speed two orders of magnitude greater than the predator and no boundary effects that could trap preys. Instead, there was a reduced number of encounters, but they were still present. This is likely caused by the combined effects of multiple predators chasing a singular prey, eventually leaving the prey with no optimal location out of the reach of the nearest predator. If just a few predators were included in the simulation, preys would easily have been able to outmaneuver each predator, but increased predator densities led to an inadvertent swarming effect, as multiple predators attacked a prey from multiple angles. These results indicate that individual-based models that incorporate motivated animal movements do not need to make a priori assumptions about swarming behavior, as it will emerge as an aggregated result of the decision-making process of each individual.

5) Despite the inclusion of prey avoidance behaviors, various magnitudes of the prey’s ability to perceive and move throughout the environment, prey density was the driving factor behind the predator-prey encounter rates. Predator’s efficiency being a function of prey density is used in most ecological studies (SOURCES), but the refined spatial scale of an individual-based paradigm prompted this investigation. An emergent feature of this individual-based framework was patchiness of prey densities. In this model, that patchiness was created both through random placements of individuals and consistent prey movements that directed preys close to a predator on a similar movement trajectory. This caused individual prey densities to have a median of (XX), and vary widely (XX–XX) among predator individuals. In pooled modeling frameworks, the prey density calculation used to derive a predator’s efficiency would have been consistent, as it would have been calculated as the quotient of the number of preys within a designated space (a constant in our one-grid-cell simulation) and the modeled area. We argue that the number of preys within a perceivable area is a more refined and accurate estimation of an individual predator’s prey density because it incorporates the potential heterogeneity of prey populations. Advanced modeling methods that apply consumption rates to energy acquisition (REFS), nutrient transport (REFS), and future behavioral decision making (REFS) should consider an individual-based calculation of prey densities when estimating predator efficiency, particularly if modeling small spatiotemporal scales.

It was anticipated that the predator would perceive 50% of the number of preys since the predator could perceive 50% of the total model domain. However, the proportion of perceivable preys was almost always less than half, leading to local predator consumption estimates that were lower than the global calculation prey densities. This is an example of Jensen’s inequality, a statistical concept where the expected value from a convex (non-linear) function is greater than or equal to the expected value from an individual sample (SOURCE). If the relationship between encounter rates and prey abundance were not influenced by external factors (prey behavior in this model) and the prey field was homogenously distributed, then the global consumption rate would be equivalent to the local consumption rate of each predator. Instead, the modulation of encounter rates by prey behavior creates divergence between the global and local consumption rate estimates. In this model, preys always made the optimal movements away from predators, creating depressed functional response curves scaled by the effectiveness of prey behavior (i.e., fast preys were better at avoiding predation). In reality, preys do not always make optimal decisions (SOURCES). The results of this model indicate that local consumption rates will be less than globally calculated consumption rates, as long as the preys are able to make an optimal decision more often than they make a detrimental decision.

# Acknowledgements

# Data Availability

* The Julia code for these simulations is available in the Supplemental Material and on Github (GITHUB REPO).

# Literature Cited

Drazen, J. C., and T. T. Sutton. 2017. Dining in the deep: the feeding ecology of deep-Sea fishes. Annual Review of Marine Science 9:337–366.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. The Memoirs of the Entomological Society of Canada 97:5–60.

Langbehn, T. J., D. L. Aksnes, S. Kaartvedt, and Ø. Fiksen. 2019. Light comfort zone in a mesopelagic fish emerges from adaptive behaviour along a latitudinal gradient. Marine Ecology Progress Series 623:161–174.

Menard, F., C. Labrune, Y.-J. Shin, A.-S. Asine, and F.-X. Bard. 2006. Opportunistic predation in tuna: a size-based approach. Marine Ecology Progress Series 323:223–231.

Spitz, J., E. Mourocq, J.-P. Leauté, J.-C. Quéro, and V. Ridoux. 2010. Prey selection by the common dolphin: Fulfilling high energy requirements with high quality food. Journal of Experimental Marine Biology and Ecology 390:73–77.

Van Den Hoff, J., C. Eriksson, H. Burton, and M. Schultz. 2018. Size-Selective Feeding by Mesopelagic Fish Can Impact Ocean Surface Abundance of Small Plastic Particles.

## Old Text

* The proper calculation of prey density is an important component as this is the greatest factor in determining the encounter rates between predator and prey compared to individual-based decisions.
  + Depending on the modeler’s decision to use the grid vs. perceived area prey density calculation
  + Although an animal’s visual field did not affect encounter rates based on prey behavior, this perception range is a valuable concept to calculate as it will directly influence the prey density calculation for each individual.
* The ratio between the prey visual range and predator visual range affected the average encounter rates.
  + When prey visual ranges were higher than the predators (i.e., the prey had the visual advantage), the predators were less likely to encounter preys than when the predator’s had an equal or greater visual range.
  + Oceanic predators are typically afforded this advantage with large eyes that contain aphakic gaps for enhanced visual acuity (SOURCE).
  + The inclusion of simulations where the prey have a greater visual field than the predator simulates the potential for non-visual cues to provide a sensory advantage to the prey.
  + In these scenarios, the prey are able to avoid the predator more frequently than when the predator has the advantage.
  + Sensory capabilities beyond assumed visual effectiveness scaled to body size are not commonly incorporated into ecosystem modeling efforts, but these results suggest that their inclusion could affect encounter rates, and subsequent functional response curves,

*Differences caused by visual acuity*

The visual acuity of the prey without the corresponding swimming velocity to outpace the predator did not have an influence on encounter rates. Although the predation procedure in this model was simple and predators were constantly motivated without limitations to their energetic expenditure, faster preys could effectively avoid predation by placing themselves further away from the predator than another prey. There are mechanistic problems with testing this hypothesis, as open-ocean predator prey dynamics are generally size-structured(Menard et al. 2006), but the differences observed suggests that the optimal avoidance algorithm was effective, so long as the preys were physically able to outpace the predator. Hypothetically, this procedure increased the foraging time of each predation event, which in a more complex simulation (e.g., three or more species, predators of predator, considerations to environmental and distance-based energetic constraints) could influence encounter rates.

*Predator swarming behavior*

Predator swarming behavior is a useful tactic for many large marine predators to increase predation efficiency by trapping preys between multiple predators that are attacking from multiple directions (SOURCES). This was not explicitly incorporated into this model algorithm. Instead, all predator individuals had an independent, but shared motivation (i.e., catching the nearest prey). Encounter rates should have been nearly absent in scenarios with a prey swimming speed two orders of magnitude greater than the predator and no boundary effects that could trap preys. Instead, there was a reduced number of encounters, but they were still present. This is likely caused by the combined effects of multiple predators chasing a singular prey, eventually leaving the prey with no optimal location out of the reach of the nearest predator. If just a few predators were included in the simulation, preys would easily have been able to outmaneuver each predator, but increased predator densities led to an inadvertent swarming effect, as multiple predators attacked a prey from multiple angles. These results indicate that individual-based models that incorporate motivated animal movements do not need to make *a priori* assumptions about swarming behavior, as it will emerge as an aggregated result of the decision-making process of each individual.

* The ability of an animal to perceive its environment affected the amplitude of the functional response curve.
  + Generally smaller organisms have a smaller visual field than larger organisms in aquatic environments because of the dependence on ocular characteristics to see underwater.
  + As light levels decreased at night, the visual field of both predator and prey dramatically declined compared to the day.
  + However, during the crepuscular period, the predator had a distinct advantage.
  + Many visual aquatic predators utilize the crepuscular period for greater foraging efficiencies (SOURCE).
  + Integrating this effect into functional response curves is necessary in multi-species individual-based models that simulate aquatic ecosystems over the duration of a 24-hour period because the changes in light levels affect the ability for a predator to forage and prey to avoid predators.
* The standard Type II functional response curve shape was retained in all of the scenarios that were conducted.

As expected, increased prey density corresponded to an increased predator-prey encounter rate, even with random vectorized movements by predators. This phenomenon occurs because of the random chance associated with a predator running into a prey. Directed prey behavior reduces the predation efficiency of predators by decreasing encounter rates, and this movement is more effective as prey swimming speeds increase. This model is limited by the uni-motivational structure of predators only consuming prey and prey only attempting to avoid predation. Mutli-species (3+) modeling approaches may provide a more complex image of the behavioral effect of functional response curves, as species would have to balance multiple priorities (e.g., choice to avoid predators or hunt preys) to maintain their energetic demand. Although this model framework was more simplistic than marine ecosystems are typically understood to be, the controlled investigation shows ecological functional response curves are not simply a function of prey density, when modeling predator-prey dynamics at an individual scale.

* Individual-prey densities ranged from zero preys within the perceivable window to XX preys with a mean value of XX (± XX).
  + Assuming a search rate of XX and handling time of XX, the predator efficiency would range between XX and XX with an average value of XX in a Type II functional response equation(Holling 1965).
  + Since the perceivable prey densities did not follow a normal distribution

Despite the inclusion of prey avoidance behaviors, various magnitudes of the prey’s ability to perceive and move throughout the environment, prey density was the driving factor behind the predator-prey encounter rates. Predator’s efficiency being a function of prey density is used in most ecological studies (SOURCES), but the refined spatial scale of an individual-based paradigm prompted this investigation. An emergent feature of this individual-based framework was patchiness of prey densities. In this model, that patchiness was created both through random placements of individuals and consistent prey movements that directed preys close to a predator on a similar movement trajectory. This caused individual prey densities to have a median of (XX), and vary widely (XX–XX) among predator individuals. In pooled modeling frameworks, the prey density calculation used to derive a predator’s efficiency would have been consistent, as it would have been calculated as the quotient of the number of preys within a designated space (a constant in our one-grid-cell simulation) and the modeled area. We argue that the number of preys within a perceivable area is a more refined and accurate estimation of an individual predator’s prey density because it incorporates the potential heterogeneity of prey populations. Trophic models aiming to simulate spatiotemporal variability in predator’ consumptive effects and energy transfer would benefit from this refined approach.

* Prey avoidance behaviors require an individual to perceive its environment, which in the open ocean, is likely limited by the animals visual acuity. In this study, the limitation of a prey to not sense the entire model domain was advantageous to the predator, exhibited by increased encounter rates when a visual range limitation was applied to the prey. Although this study only tested limitations to visual acuity, other sensory perceptions (e.g., chemosensory, acoustic) are prevalent in open-ocean ecosystems. Although it is unlikely that a single prey could pinpoint the exact location of a predator, this simulation suggests that the reliance on alternative, non-visual sensory abilities may be a greater advantage to the predator avoidance behavior of small, oceanic animals aiming to avoid predation by visual predators
* The logarithmic relationship between encounter rates and the relationship between predator and prey speeds suggests there is may be selective limitation for pelagic species to increase their swimming speed without additional pressure. For example, the inflection point of this relationship is near the 1:1 ratio, meaning that if predator and prey are currently capable of swimming the same speed, increased velocities by either predator or prey will have a large effect on the predation efficiency of the predator. This slope is less steep beyond one order of magnitude, indicating that if a predator is currently one order of magnitude faster than its prey (in terms of meters s-1 estimates), then the development cost of the predator becoming faster may not be worth the limited enhancement to its foraging efficiency.
* Ecosystem models that estimate high-trophic level processes require a mechanistic understanding of ecological functional response curves, which are reliant on encounter rates. Encounter rates are influenced by prey densities (SOURCE), but in this study, we show that a predator’s feeding efficiency is also influenced by the relationship between predator and prey swimming velocities, behavior, and each animal’s ability to perceive the environment (i.e., visual range). This model does not consider refuge effects or shoaling behaviors, which would bias the advantage between prey and predator, respectively.
* Unlike benthic environments, pelagic ecosystems do not have structural refuge, with the exception of floating debris (SOURCES) and pelagic algae (e.g., *Sargassum* sp.). Yet pelagic animals are still limited by their ability to perceive the environment, which varies as a function of light attenuation, the sensory capabilities of the predator, and the luminescent properties of the prey (Aksnes et al.; Nillsen et al.). Larger predators are more adept at visually perceiving a larger area pelagic environments than smaller animals, particularly in low-light environments (SOURCES). In this study differences in light levels resulted in predators having a greater advantage during the crepuscular period than during the day, and the advantage was the visual advantage was the weakest during the night because the visual range of the predator varied more on a diel scale (range: XX–XX) than the prey (range: XX–XX). Therefore, small species in the pelagic environment that are aiming to avoid predation by larger, actively hunting predators will be safer from predation during night than day and crepuscular periods.