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

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# 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 density-dependent, hyperbolic function of the surrounding prey density, handling time, digestion rates, and satiation of the predator, which influence encounter rates (Jeschke et al. 2002, Li et al. 2018, Papanikolaou et al. 2020). Changes to prey density results in a non-linear adjustment to a predator's estimated consumption rate, commonly termed ecological functional response curves (Holling 1965). Several variations of these functional response curves have been established to more accurately model predator foraging rates, with variations according to food-web complexity (Chan et al. 2017), predator density (Cosner et al. 1999, Kratina et al. 2009), and habitat complexity (Grabowski 2004), among others. Animals alter their behavior when presented with potential threats in ways that affect predator-prey encounter rates, predator consumption effects, and energy landscapes in marine ecosystems (Preisser et al. 2005, Papastamatiou et al. 2023). Animals must be able to avoid these threats in an environment where the predator has an alternative goal of increasing its predation success. The relative sensory capabilities (e.g., vision) that allow both predator and prey to perceive their environment and the swimming velocities will likely determine the influence of these behaviors on encounter rates. Swimming velocities roughly correspond to their body shape, body size, and additional characteristics (e.g., scombrid keels), which affect the animal’s ability to reduce drag and produce thrust in a viscous medium (Liao 2007). A prey’s ability to both perceive and avoid predators could lead to reduced encounter rates compared to preys that cannot avoid predation, resulting in a dampened functional response curve and reduction in the theoretical foraging efficiency of a predator.

Despite the explored variations in functional responses, many popular food-web models are not capable of simulating populations at the individual scale, and thus cannot incorporate individual-based factors that influence functional response curves. Instead, simplistic versions of these functional response curves are utilized, largely making these assumptions based on static (i.e., not changing after calibration) state parameters and spatiotemporally dynamic prey densities (SOURCES). Novel food-web modeling approaches are being developed with faster programming speeds (e.g., Julia Programming Language; ), creating the possibility for individual-based modeling (Wu and Forget 2022). 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.

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 perceive 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 foraging efficiencies, which could then be aggregated to the species-level with quantified variance (Figure 1).

A screenshot of a video game

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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.

In this study, we developed a three-dimensional, two-species model to examine changes in the encounter rates of predators and preys among a range of prey abundances, swimming velocities, and visual ranges. Functional response curves emerged as the relationship between encounter rates 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 and this effect was integrated into a novel ecological functional response curve equation. Predator-specific prey densities were 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 100 meters x 100 meters x 100 meters cube (1,000,000 cubic meters in volume) with no structural habitat, best simulating a pelagic environment. Only active movement (i.e., swimming) was considered 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 with a scalar movement velocity vector during each simulation (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 | 100 | 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 | 49.2 | 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 (49.2 m radius; i.e., half of the model domain volume), predator abundance (n = 100 individuals), and predator handling time (8 minutes) were the same in each simulation. In this study, the handling time parameter is considered to also include digestion time. 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 a particular predator-prey interaction, but instead are designed to explore how encounter rates vary with respect to relative differences in predator/prey characteristics. 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 continued for 300 minutes at a one-minute scale. The encounter rate (N encounters timestep-1) was calculated for each simulation and comparisons were made among prey velocities, visual fields, and abundances.

The modeled prey abundances (*P*), handling time (*h*), and emergent encounter rates (*enc*) were utilized to estimate the optimal effective attack rate (*a*) for each prey swimming velocity and visual range pair (Equation 1). The optimization was completed using the R programming language and the *optim()* function in the “stats” package (R Core Team 2023) with a starting *a* value of 0.01 and potential range of 0–5000. All iterations were able to converge, but simulations with a RMSE greater than XX were removed, as they did not follow the appropriate Type II functional response curve. All the removed functional response curves had less than 0.01 encounters timestep-1, regardless of the modeled prey abundance. The estimated effective attack rates were compared among prey swimming velocities and visual ranges.

(1)

Two prey densities 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. The number of preys within each predator's perceivable area was recorded during the last timestep of each simulation. 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 2).

(1)

where the encounter rate is derived from equation 1 with the newly acquired local prey densities, estimated attack rate, and same handing time parameter. A predator success coefficient (*pc*; 0.7), prey weight (*w*; 5 g), and prey energy density (*d*; 5,000 J) convert the estimated encounter rate to the possible biomass consumed during that time step. Although the initial model assumed predators 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 represented those that may be realistic for this model domain, but could be any, as they 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

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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.

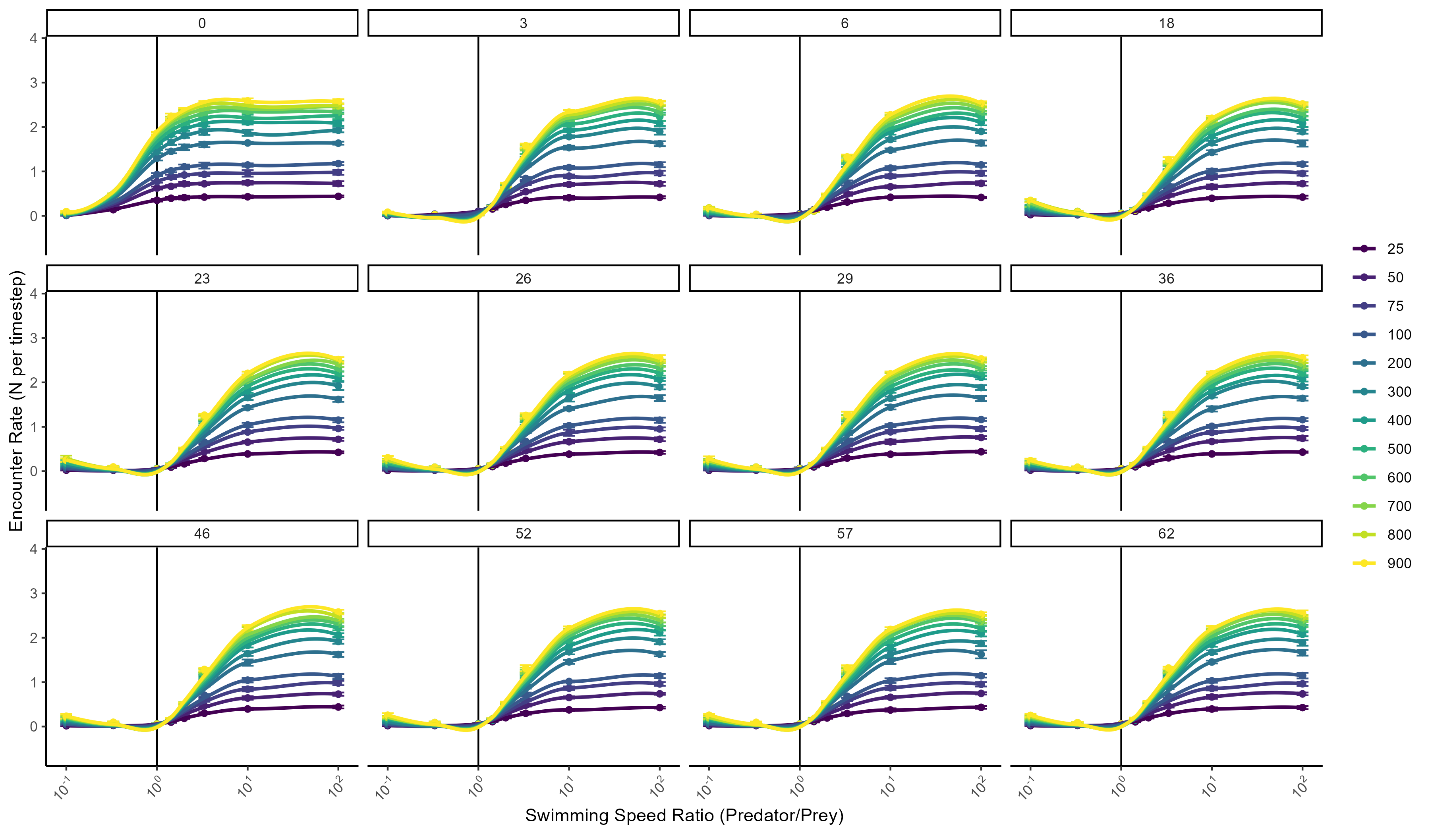


Figure . The relationship between predator-prey encounter rates and predator-prey relative swimming velocities (log-transformed). Prey abundances are represented as colors and prey visual range (visual distance; m) are represented as facets. Predator velocity (0.01 m s-1; vertical black line), abundance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

## New FR Curve Equation

The relative swimming velocity between predator and prey and visual range had an influence on the attack rate coefficient (*a*) of the functional response curve (Table 2). Preys that were 10x faster than their predator did not align with a Type II functional response curve because they could effectively avoid most encounters at all prey abundances. Preys that could see greater than 3 m or further had similar attack rate coefficients when compared to simulations of the same swimming velocity and only followed a Type II response curve if the predator was at least twice as fast as the prey. Preys that could perceive their environment had a smaller attack rate coefficient than blind preys for swimming velocity ratios between 2:1–10:1 (Table 2). There was a 6-fold difference in the attack rate for swimming ratios of 100:1 and 2:1 (Table 2). Blind preys were less successful than visual preys at modulating predator attack rates (Table 2). Differing predator attack rates among varying prey swim velocities indicate that the estimated individual-based consumption rate will be different based on the prey’s ability to avoid predation.

Table . The attack rate coefficients (*a*) for a Type II functional response curve that correspond to the encounter rates. All preys that could see (Visual distance greater than 0) had the same attack rate coefficients. Only pairs that had converged *a* values are reported

|  |  |  |
| --- | --- | --- |
| **Relative Swim Speed** | **Blind** | **Not Blind** |
| 0.1 | - | - |
| 0.3 | 0.001 | - |
| 1.0 | 0.004 | - |
| 1.4 | 0.005 | - |
| 2.0 | 0.005 | 0.001 |
| 3.3 | 0.006 | 0.003 |
| 10.0 | 0.006 | 0.005 |
| 100.0 | 0.006 | 0.006 |

## 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 1–12). In a homogenous environment where the predator can perceive 50% of the volume, it would be 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 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.

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Figure . Ridgeline plots of A) the number of preys within each predator's perceivable area B) and the proportion of available preys within the model domain that were within the perceivable range of the predator. These results only reflect the scenarios where prey velocity was equivalent to the predator and visual range was 46 m. 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 1-12.

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 3.9–29.7 J timestep-1, depending on the prey abundance (Figure 5). The local estimates had minimum and maximum values of 0.3 and 29.6 J timestep-1, respectively (Figure 5). Comparing the different swimming velocities and visual ranges, the 95% confidence ribbons of consumption from the local densities were similar. The variance in these confidence intervals ranges from 1.3 J timestep-1 to 20.4 J timestep-1 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.

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Figure . The consumption rates derived as a function of prey density encounter rates as a function of prey abundance. Relationships are divided among all relative swimming velocity (columns) and prey visual ranges greater than 0 m (rows) that followed a Type II response curve. Both grid-based response curves (red line) and individual-based response curves (black ribbon) are shown.

# Discussion

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. Predator-prey encounter rates are primarily influenced by prey density and lead to the emergence of a Type II ecological functional curve in all simulations where the predator was faster than the prey. Enhanced prey defense abilities in protist communities also reduces the asymptote of functional response curves and switches the overall shape from a Type II to a Type III functional response (Hammill et al. 2010). This study did not incorporate physical habitat structure, which can provide prey refuge and affect predator successes, as long as the predators cannot successfully navigate the habit (Anderson 2001, Mattila et al. 2008). This type of structure is nearly absent in pelagic, open-ocean environments, with the exception of the sporadic floating debris and *Sargassum* mats. Therefore, the simulations in this study are most representative of open-ocean ecosystems and it is most likely that predator-prey relationships in these ecosystems can be predicted using Type II ecological functional response curves. However, the steepness and asymptotes of these curves were influenced by prey behavior. The explicit modeling of individual predator and prey behaviors produced different encounter rates than would be expected through a standard calculation-based prey abundance in a defined area.

The trophic level of carnivorous fishes scales positively with body size (Keppeler et al. 2020) and many open-ocean species follow 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. Additionally marine predators are often faster than prey because of the physical advantage of being a larger object moving through a liquid medium (Domenici 2001). In this study, there was a dramatic decline in encounter rate estimates between the swimming velocity ratios 10:1 (i.e., predator is 10x faster than prey) – 1:1 (predator and prey have equal velocities, and little difference between ratios of 100:1–10:1 and 1:1–1:10. The encounter rates in a predator prey interaction are related to the relative swimming speed (Evans 1989), and this can be further influenced by turbulence for microscopic organisms (Rothschild and Osborn 1988). This study indicates that there is a limitation to this influence on encounter rates, where predators that are currently 10x faster than their prey would not benefit from becoming faster, and *vice versa*. Additionally, the effect of relative swimming speed on encounter rates grows with increasing prey abundances until the prey abundance at which the functional response curve reaches an asymptote. Prey behavior is capable of modulating encounter rates in marine ecosystems, and this should be considered when utilizing equations to model encounter rates in individual-based assessments.

The effect of relative swimming velocity on encounter rates was enhanced when preys could visualize their environment and make informed movement decisions, rather than moving at a random vector. A visual distance of three meters, compared to 49 meters for the predator, allowed for preys that were 1/3 of the swimming speed as the predator to decrease encounter rates by *c.* 50%. Increasing the prey visual range beyond three meters did not have as large of an impact on the functional response curve, suggesting this effect is only relevant at small scales. Hypothetically, the optimal foraging procedure also increased the foraging time of each successful predation event, as predators had to catch preys moving away from them. The visual acuity of marine fishes is related to eye size, and not necessarily body size (Caves et al. 2017), but vision is also necessary for reasons beyond predator avoidance that were not examined here (e.g., mate choice). In a more complex simulation (e.g., three or more species, multiple predator or prey species, considerations to environmental and distance-based energetic constraints) enhanced visual capabilities could have a greater influence on predator avoidance success, as individual preys would have to adjust their optimal foraging strategy at each time step.

Group predation tactics are used by many marine predators to increase predation efficiency by trapping preys between multiple predators that are attacking from multiple directions (Heithaus and Dill 2009). This was not explicitly incorporated into this model algorithm and 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.

It was anticipated that the predator would perceive 50% of the modeled 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 (McShane 1937). 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). However, preys are not likely to always make optimal decisions, and the effects of this result should be seen as optimistic in favor of the prey. 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.

An emergent feature of this individual-based framework was patchiness of prey densities. 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 vary widely among predator individuals and this variance to grow with increasing prey density. The energetic trade-offs associated with patchy prey environments influence the optimal movement speed for a predator, and in extreme cases, survivability (Zollner and Lima 2005). This generally leads to predators being distributed according to an Ideal Free Distribution, which is a learned behavior where an individual predator is most likely to situate itself near a patch that maximizes its encounter rate (Fretwell and Lucas 1970, Kacelnik et al. 1992). Despite the theoretical backing of this approach, modeling frameworks with pooled populations often simulate spatial scales that are coarser than an individual’s perceivable 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 and integrates a fairer assessment of an Ideal Free Distribution than considering areas larger (or smaller) than each predator can interact in a given timestep. Advanced modeling methods that consider individual animal decisions should consider a local calculation of prey densities when estimating predator efficiency.

# Acknowledgements

# Data Availability

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

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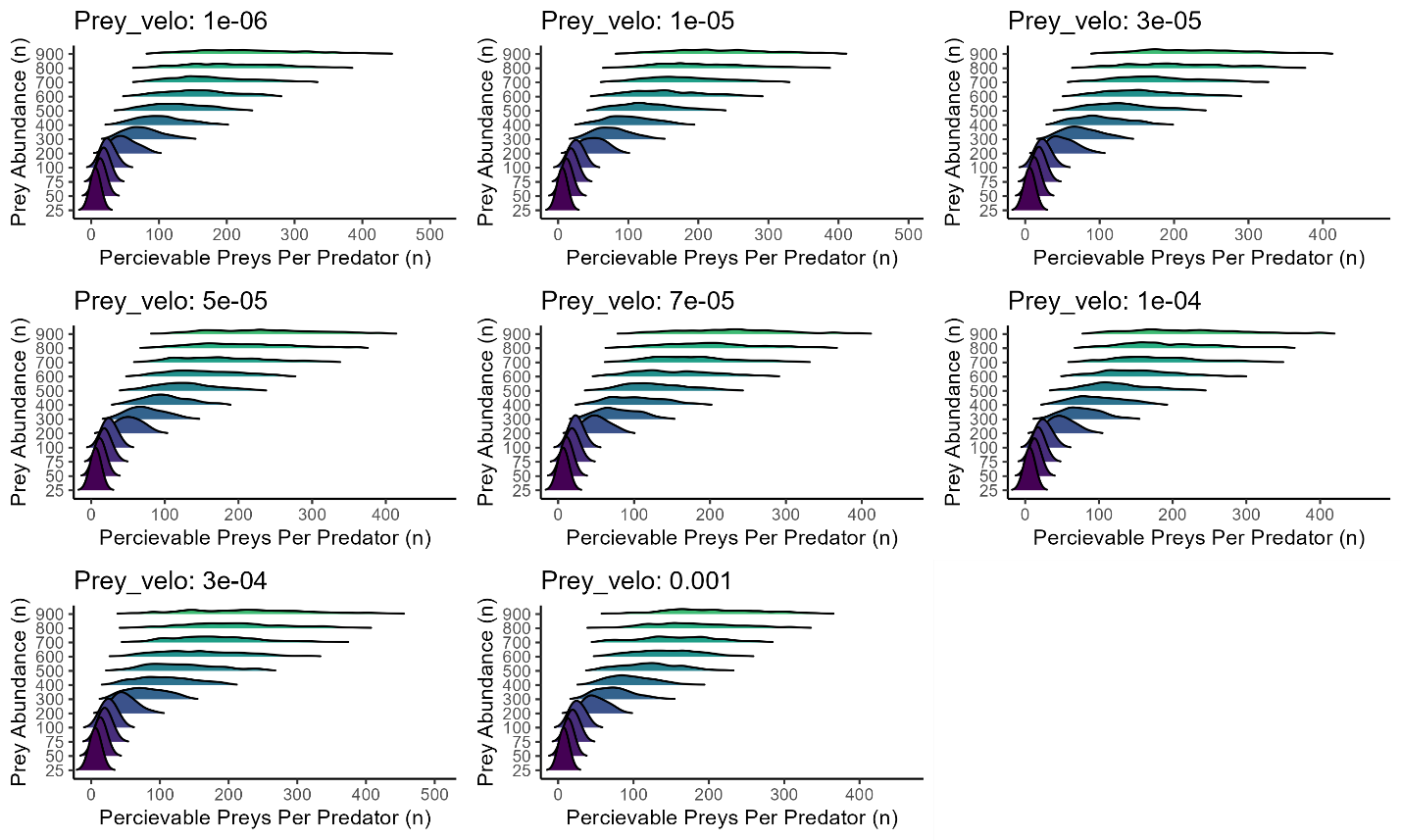
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# Appendix

The following plots are all renditions of Figure 4A at different prey swimming velocities (panels) and visual ranges (full figures ordered smallest visual area to largest)

A graph of a number of numbers

Description automatically generated with medium confidenceA graph of a number of numbers

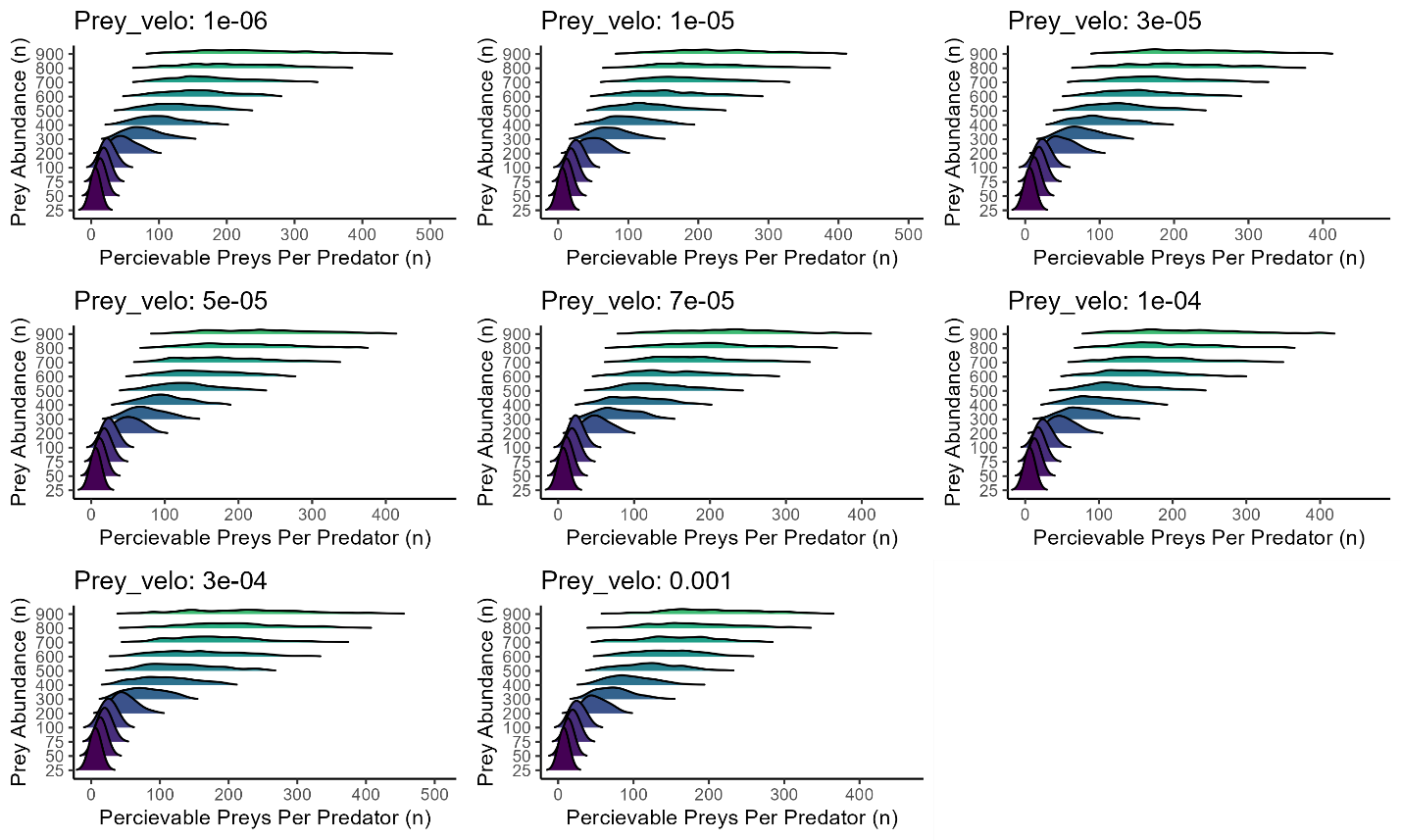
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