**Individual-based modeling reveals that predator-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 and various ecological and ethological factors that cause limitations to the foraging capacity of the predator. Food-web models rely on predation efficiency estimates to calculate consumption rates, but these models often lack the resolution to consider predators as individual entities with different predation success rates. Individual-based modeling can provide this resolution and is becoming more tenable as computational power increases. 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 consumption rates. Encounter rates followed a Type II ecological functional response curve (hyperbolic curve) for all simulations where the predator was at least twice as fast as the prey. The effective attack rate of the predator was influenced by the relative swimming velocity between predator and prey, and partially by the prey’s visual ability, affecting the steepness and asymptote of the functional response curve. Although each predator could perceive half of the model domain volume, the number of preys within each predator’s visual range (i.e., local prey density) was almost always less than half in all simulations, indicating that the emergent prey field was heterogeneous. The consumption rate estimates from local prey densities were less than global prey densities, and local prey densities among all predators had variance scaled to the modeled prey abundance. Local prey densities are a necessary calculation for individual-based predator/prey models because they provide refined consumption rate estimates based the immediate surrounding prey field with considerations to behavioral impacts that modulate predator/prey dynamics. Heterogeneous prey fields and individual behavioral decisions modulate predator-prey dynamics, which can only be modeled with an individual-based model.

**Keywords:** Predator/prey dynamics, Individual-based modeling, Food webs, Functional Responses, Theoretical Modeling, Agent-based 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-additive adjustment to a predator's estimated consumption rate, commonly termed ecological functional response curves (Holling 1965). Several variations of functional response curves have provided a more refined understanding of 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. Moreover, animals alter their behavior when presented with potential threats in ways that affect predator-prey encounter rates, population-scale consumptive impacts, and energy landscapes in marine ecosystems (Preisser et al. 2005, Papastamatiou et al. 2023). Animals attempt to avoid these threats in an environment where the predator has the opposite goal of increasing predation success. Sensory capabilities (e.g., vision) that allow both predator and prey to perceive their environment and 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) that reduce drag and produce thrust in a viscous medium (Liao 2007). Predator avoidance mechanisms could lead to reduced encounter rates compared to preys that cannot avoid predation, resulting in a dampened functional response curve and reduction in the foraging efficiency of a predator.

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 functional response curves are utilized, largely making assumptions based on static (i.e., not changing after calibration) state parameters and gridded prey densities. Agent-based models (i.e., individual-based models) are capable of simulating populations at the individual scale and explicitly modeling informed animal decisions (Thiele et al. 2011). Their utilization into complex ecological modeling techniques has been limited by the computational expense of explicitly modeling individuals at large, but fine, spatiotemporal scales. This computational limitation leads necessitates parameter aggregation for those less important to the central model question (Plagányi et al. 2014), which could be sufficient in certain situations. However, there is strong logic behind incorporating species’ traits and size structure in ecosystem-scale modelling efforts (Blanchard et al. 2017, Weisberg et al. 2024), which requires refined individual-scale modeling approaches. Novel ecological network analysis methodologies are being developed with faster programming speeds using the Julia Programming Language (Banville et al. 2021), creating the possibility for individual-based modeling of ecosystems at fine spatiotemporal scales (Wu and Forget 2022). The application of an individual-based model as an ecosystem-scale food-web model requires a mechanistic understanding of how individual animal decisions may influence a predator’s foraging efficiency and subsequent consumption rates.

Marine populations are often organized as heterogenous patches, were individuals are tightly aggregated in locations at higher densities than the background density (Levin 1994). This patchiness influences future animal movements as predators perceive prey patches and orient themselves within areas of high prey density, ostensibly to increase foraging success (Kacelnik et al. 1992). Each predator individual could experience different prey densities, and subsequent encounter rates. However, food-web models are often applied at singular spatial scales (i.e., the same spatial scale for each species/functional group) and that spatial scale is likely different than an individual predator could perceive within a defined temporal scale. This mismatch limits the model’s ability to simulate the patchiness that emerges from fluid dynamics and animal movements. 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 (Figure 1). These individual calculations, and the processes that determine differences among predator individuals, can only be simulated using an individual-based model.

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 these effects were quantified as an adjustment to the effective attack rate of the predator. Predator-specific prey densities were calculated as both a grid-based density (global) and individual-based density (local) and consumption rate estimates were derived from both.

# Methods

## Model Structure

Predator-prey encounter rates were examined using a modified version of *PlanktonIndividuals.jl* (Wu et al. 2022) that allowed for 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 a scalar movement velocity 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* |  |  |
| Prey Weight | 5 | g |
| Prey Energy Density | 5,000 | Joules |
| Predator Capture Success | 0.7 | Dimensionless |

## Simulations

The predator-prey encounter rates were estimated as a function of prey abundance (25–900 individuals at varying intervals), prey velocity (0.0001–1 m s-1), and prey visual range (0–62.04 m radius; Table 1). Predator velocity (0.01 m s-1), predator visual range (49.2 m radius; half of the model domain volume), predator abundance (n = 100 individuals), and predator handling time (8 minutes) were the same in each simulation. The handling time parameter was 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 ranges were chosen to provide a relative representation of two hypothetical species. Since these parameters would vary with species’ morphology and visual capabilities, these parameters did not necessary represent a particular predator-prey interaction, but instead were designed to explore how encounter rates change 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 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 moved towards the closest prey and the prey moved 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 towards a random vector at a distance consistent with their swimming velocity. When predators reached preys (1 m threshold distance), consumption occurred, and an eight-minute handling time was applied to that predator. The simulation continued for 300 minutes at a one-minute temporal resolution. 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 0–5,000. All iterations converged, but simulations with a RMSE greater than 5 encounters timestep-1 predator-1 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 optimal 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. 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. The last timestep reflected the combined effects of each individual’s preceding animal movements and was considered 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 for simulations that had an optimal effective attack rate (Equation 2).

(2)

where the encounter rate is derived from equation 1 with the newly acquired local prey densities, estimated attack rate, and same handing time parameters. A predator success coefficient (*pc*; 0.7), prey weight (*w*; 5 g), and prey energy density (*d*; 5,000 J) converted the estimated encounter rate to the biomass consumed during that time step. Although the initial model assumed predators were always successful, a value of 0.7 was considered more realistic (Langbehn et al. 2019) 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 predator-prey encounter rates were a function of prey density and followed a Type II ecological functional response curve, when predators were at least twice as fast as prey (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) than when preys could perceive the environment, comparing simulations of the same prey velocity and abundance (Figure 2). 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 range had little effect on the predator/prey encounter rate (Figure 2). Prey density and prey velocity had 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 had limited influence.

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 (Figure 3). 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). When preys are capable of seeing predators and are 10x faster than the predator, the encounter rates are not different among modeled prey abundances. An inflection point occured 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 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.

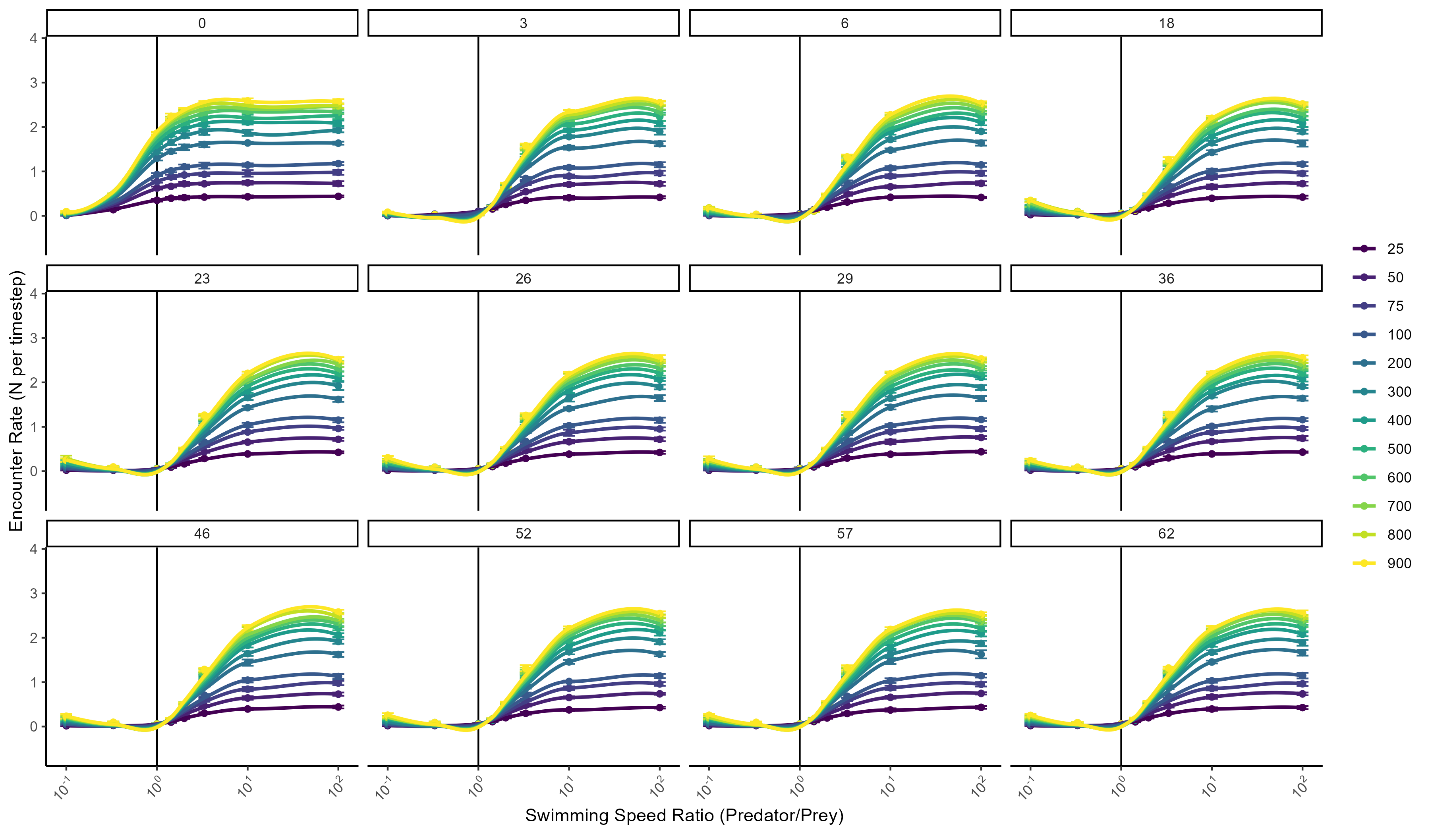


Figure . The relationship between predator-prey encounter rates and predator-prey relative swimming velocities (log-transformed). Prey abundances are represented as colors and prey visual range (visual distance; m) are represented as facets. Predator velocity (0.01 m s-1; vertical black line), abundance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

The relative swimming velocity 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, independent of visual ability. Preys that could see greater than 3 m or further had similar attack rate coefficients when compared to simulations of the same swimming velocity. There was a 6-fold difference in the attack rate for swimming ratios of 100:1 and 2:1 when preys were not blind, but blind preys were less successful 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 effective attack rate coefficients (*a*) for a Type II functional response curve that correspond to the emergent encounter rates. All preys that were not blind (Visual distance greater than 0) had the same attack rate coefficients for the corresponding swimming speed. Pairs with a RSME greater than 5 encounters timestep-1 predator-1 (i.e., not a Type II response curve) were not considered (“-“)

|  |  |  |
| --- | --- | --- |
| **Relative Swim Speed** | **Blind** | **Not Blind** |
| 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 (local prey density) was greatest at high prey abundances than at low prey abundances for all prey swimming velocity and prey visual range combinations (Figure 4A; Supplemental Figures 1–12). In a homogenous environment, it would be expected that the predator could perceive 50% of all available preys, matching the visual field of the predator. However, the local prey densities peaked between 20% and 45% per predator among all the prey abundance scenarios (Figure 4B). There is a positive linear relationship between prey abundance (p < 0.001 for all pairs) and the variance local prey density with goodness of fit values that ranging 0.8–1.0 (Figure 4C; Supplemental Figure 13). 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 close-up of a graph

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Figure . Ridgeline plots of A) the number of preys within each predator's perceivable area and B) 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 variance (± 1 standard deviation) of the local prey density and prey abundance separated by prey swimming velocity (colors) and prey visual range (facets). Only four prey visual distances are represented, since all visual ranges were similar. All other relationships are in Supplemental Figures 1-13.

The emergent effective attack rates and prey densities resulted in global density consumption rate estimates (*Cglobal*) and local density consumption rate estimates (*Clocal*) that varied among prey swimming velocities and visual ranges (Figure 5). The largest effective attack rate (0.006; Table 2) led to the highest asymptote in the *Cglobal* curve (26.3 J timestep-1 predator-1; Figure 5), while the lowest effective attack rate (0.001; Table 2) resulted in the lowest asymptote of the *Cglobal* calculation (8.0 J timestep-1 predator-1; Figure 5). Since the *Cglobal* calculation involved two constants (number of preys within the model domain, model domain volume), there was no within-simulation variance. The *Clocal* estimates were consistently lower than the *Cglobal* estimates, and this difference increased with increasing modeled prey abundance (Figure 5). At the highest prey abundance (n = 900 individuals), the difference in *Cglobal* and the median of *Clocal* ranged from 3.3–6.8 J timestep-1 predator-1. The variance in the *Clocal* confidence interval increased with increasing prey abundance, ranging from 0.2–15.2 J timestep-1 predator-1 (Figure 5). The differences in *Cglobal* and *Clocal* as well as differences among predator individuals are anticipated to accumulate and create a greater potential for erroneous population-scale consumption rate estimates.

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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 (gray ribbon) are shown. The black line corresponds to the median of the local consumption rates.

# Discussion

Predator-prey encounter rates are primarily influenced by prey density and, in this simplistic ecosystem, leads to the emergence of a Type II ecological functional curve when the predator is faster than the prey. The inclusion of prey behavior through varying swimming velocities, visual ranges, and an optimal prey movement algorithm shows that individual animal behavioral decisions affect these functional response curves. 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 (e.g., gape size) mean mobile predators generally feed upon preys smaller than themselves. Similarly, 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 rates between the swimming velocity ratios 10:1 (i.e., predator is 10x faster than prey) and 1:1 (predator and prey have equal velocities), and little difference between ratios of 100:1–10:1 and 1:1–1:10. Therefore, 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. In reality, animals accelerate or decelerate between cruise and burst velocities according to a gaussian function, with turbulence also affecting the acceleration/deceleration of small organisms (Rothschild and Osborn 1988, Evans 1989). Considering that predator and prey would likely have offsetting cruise and burst velocities, as well as reaction times to recognize the other individual’s movement, the inclusion of dynamic swimming velocities would likely add to the encounter rate variance quantified in this study. 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 predator-prey encounter rates was enhanced when preys could perceive their environment and make informed movement decisions, rather than moving at a random vector. The visual acuity of marine fishes is related to eye size, which varies widely in the open-ocean realm (Caves et al. 2017). However, increasing the prey visual range beyond three meters had a negligible impact on the functional response curve, suggesting visual range for the purposes at predator avoidance is only relevant at small scales. In a more complex simulation where animals have multiple motivations (e.g., three or more species, multiple predator or prey species, considerations to environmental and distance-based energetic constraints) and predator swim velocity is dynamic, enhanced visual capabilities may have a greater influence on predator avoidance success, as individuals would have to prioritize their optimal movement strategies.

Encounter rates should have been absent in scenarios with a prey swimming speed greater than the predator, optimal movements, and no boundary effects that could trap preys. Instead, multiple predators with an independent, shared motivation eventually left a small number of preys with no optimal location away from the nearest predator, creating an encounter. Cooperative foraging strategies are used by many marine predators to increase the predation efficiency of individuals (Heithaus and Dill 2009, Hansen et al. 2022). This tactic was not explicitly incorporated into this model, but the effect still existed. Individual-based models that incorporate motivated animal movements do not need to make *a priori* assumptions about cooperative foraging behaviors, as they will emerge as an aggregated result of the decision-making process of each individual.

An emergent feature of this individual-based framework was patchiness of preys created through random placements of individuals and consistent prey movements away from predators. The energetic trade-offs associated with patchy prey environments influence optimal predator movements and survivability (Zollner and Lima 2005). This leads to predators being distributed according to an Ideal Free Distribution, a learned behavior where an individual predator is most likely to situate itself near a patch that maximizes its prey encounter rates (Fretwell and Lucas 1970, Kacelnik et al. 1992). High prey abundances lead to increased variance in this patchiness effect, meaning that the local prey density and variance among individual predators is dynamic with changes to prey abundance, a factor that could only be explored when explicitly modeling individual predator efficiencies. Moreover, the difference in globally and locally derived consumption estimates 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). Since predators are able to associate with prey patches (Benoit-Bird et al. 2013) and these patches have an effect on individual consumption rates, we argue that local prey density is a more accurate metric than global prey density and should be utilized in advanced food-web modeling efforts.

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# Data Availability

The Julia code for these simulations is available in a public GitHub repository (<https://github.com/fishesofthedeep/EncounterRates>) and available upon request by the authors. All input parameters for the model are listed in the Methods section and embedded within the model code.

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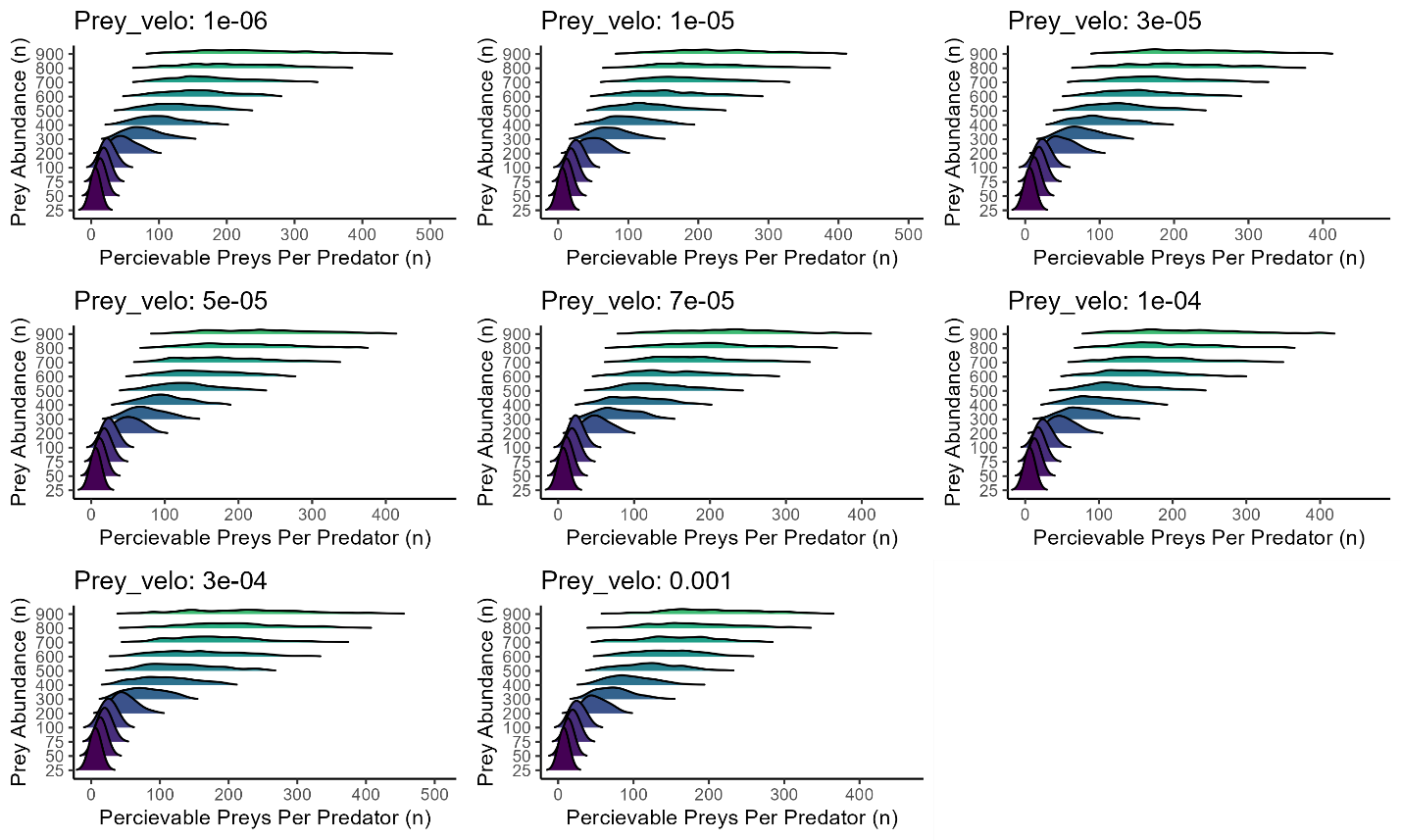
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# Supplementary Material

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

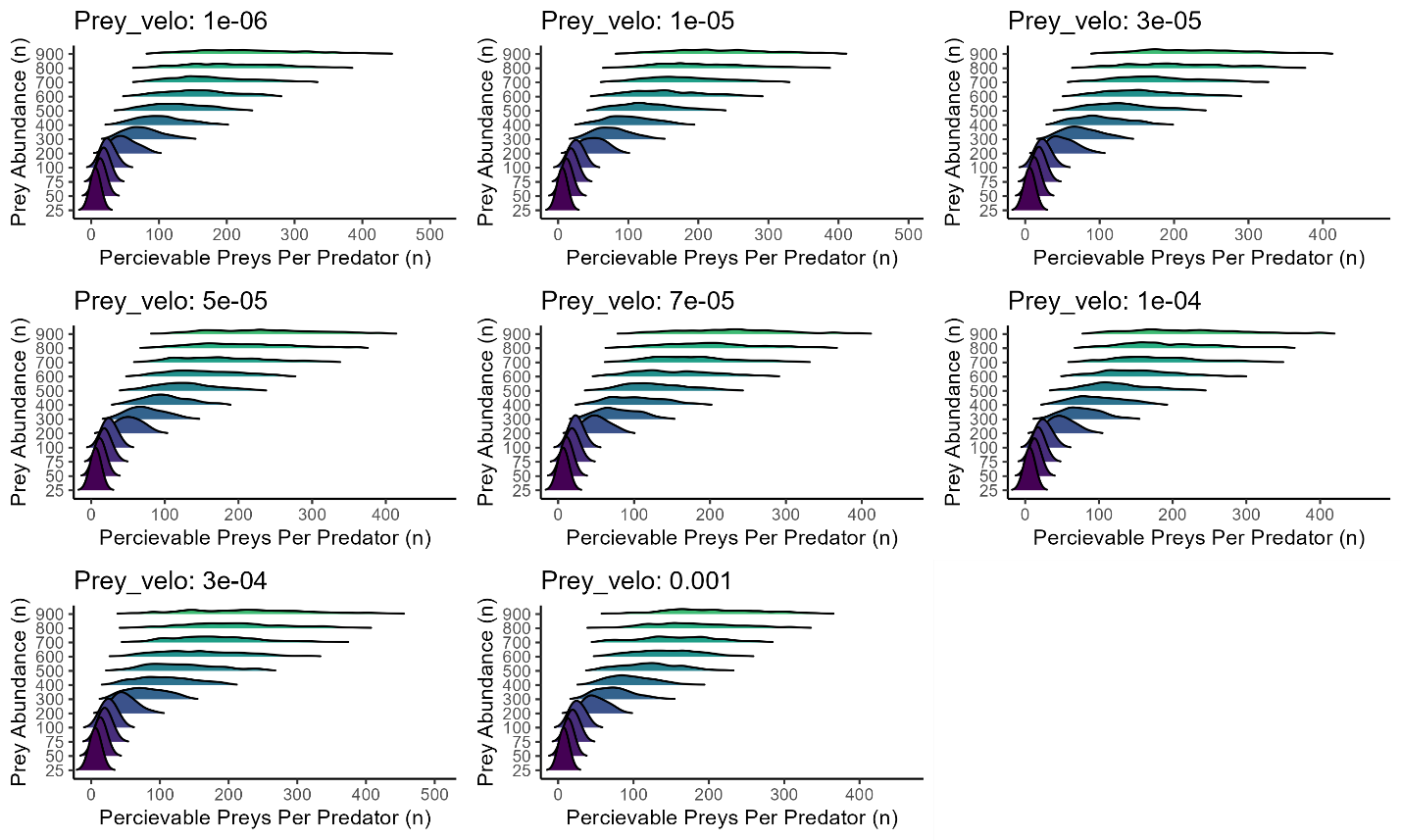
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Supplemental Figure 13. The variance in local prey densities as a function of modeled prey abundance.

A group of graphs showing different colors

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