***SwimmingIndividuals.jl*: An individual-based ecosystem model to investigate spatially explicit food webs, bioenergetic rates, and energy budgets**

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**Statement of Need**

High trophic level ecosystem models that integrate biogeochemical, biophysical, and biological processes (i.e., ecosystem models, hereafter) are becoming more readily utilized in marine resource management as there is growing evidence that predator and prey populations, and environmental factors, modulate population dynamics that cannot be explicitly resolved with single-species methods. Traditional ecosystem models simulate the biomass trends of all species in an ecosystem, and associated effects to secondary rates (e.g., predation impacts, fisheries production). Aggregated “functional groups” of similar species are often created to minimize the computational expense, or taxonomic resolution is replaced by size classes following macroecological theory. This aggregation, even if carefully chosen, removes the influence of species-specific traits that influence biological traits and community structure1. Given the vastness of marine ecosystems, traditional ecosystem models often have coarse spatial resolutions that disallow the fine-scale movements associated with behavioral impacts, which modulate predator/prey dynamics2.

An area where ecosystem models could be developed further is the inclusion of individual behavioral decisions, which allows for individual-scale calculations of bioenergetic rates and energy budgets. Nekton (i.e., animals capable of swimming against a current) somatic maintenance costs are dependent on temperature and activity rates3, which suggest that animal behavior is necessary to accurately calculate metabolic costs. The decision for an animal to move towards a prey or away from a predator has energetic consequences, which if not surmounted for by successful feeding may reduce a predator’s body condition, motivate the individual to make riskier decisions (i.e., attempt to catch prey instead of avoid predators), and potentially lead to starvation or a higher risk of predation mortality. Extending off of this framework is research questions surrounding the influence of prey quality, climate change, disturbances, etc. on individuals, which are effects that can be aggregated to the population, community, and ecosystem scale to compare to traditional ecosystem modeling metrics.

**Summary**

*SwimmingIndividuals.jl* is three-dimensional, individual-based food web model that operates at a flexible spatiotemporal scale, defined by the user. The core purpose of *SwimmingIndividuals.jl* is to predict individual animal behavior decisions in coordination with species-specific traits to calculate the bioenergetic rates and energy budget for each individual. There are two types of species in a *SwimmingIndividuals.jl* model: focal species and non-focal species. Focal species are explicitly modeled as individuals and are intended to be of predominant species type used by the user. Each individual has a unique identity (i.e., body size, location) and has biological characteristics that match the user (Table 1). Non-focal species are similar to functional groups in the traditional ecosystem modeling frameworks. Since *SwimmingIndividuals.jl* does not simulate biogeochemical processes, non-focal species are necessary so the entire ecosystem does not starve, but also serves as an option for the user to not model all species as an individual because of lack of reliable data or computing power.

The software has been developed in the Julia Programming Language, and utilizes JIT compiling performance for rapid computing speeds and the capability for enhanced performance on high-performance computing. *SwimmingIndividuals.jl* uses several packages from *PlanktonIndividuals.jl*4, an individual-based plankton ecosystem model that has both CPU and GPU capabilities. *SwimmingIndividuals.jl* is not yet compatible with GPU processing because of the need for indexing in several functions to identify individuals. Users input data through .csv files, and it is recommended that they follow the same structure as the examples. *SwimmingIndividuals.jl* uses threading where possible to speed up the processing, particularly on high performance computing clusters.

Once the model has been initialized, it will progress at a one-minute temporal resolution for the number of iterations the user requests. Non-focal species predation, growth, and mortality occurs each minute, with rations aligning to the user provided rate (% bodyweight consumed daily) standardized to one minute. Non-focal species thus feed at every time step, so species with a diel feeding pattern of interest to the research question should be modeled as focal species. This feeding acts to remove focal and non-focal species individuals based on their relative densities. For example, if the density of focal individuals (# m-3) is greater than the density of non-focal individuals, the predator species will consume a focal individual, and *vise versa*. All potential preys considered in these densities are within a predator-prey size ratio of 1%–10% of the minimum and maximum predator body size, respectively, creating a wide range of potential preys. Consumed focal individuals are removed from the model and the necessary outputs (predation mortality, diet matrix) are updated. Since predation by non-focal species is size-driven, species with considerable range in their minimum and maximum size may be separated in size classes to refine feeding by non-focal species. This approach should be used with some caution, as there is no mechanism for small conspecifics to ascend to larger size classes (e.g., recruitment) in a multi-year simulation. Non-focal species begin at a density provided by the user (# m-2) and this density is allocated to a grid that aligns the preferred output grid of the user, such that the model recognizes the number of individuals per grid cell. When predated upon, the number of individuals within each grid cell decreases, and the number of individuals grows based on a user-defined population growth rate at each time step. This population decline and growth allows for important prey groups to be dynamic. There is currently no mixing between grid cells for non-focal species, so *SwimmingIndividuals.jl* treats each grid cell akin to a separate species for population modeling purposes. Future iterations could transfer individuals between grid cells in an Eulerian pattern.

Focal species individuals operate at a temporal resolution decided by the user. This methodology allows the user to model different species at different temporal scales (minimum = 1 min.) to best capture the operational resolution of the species necessary to answer the research question and save on the computational expense of unnecessary calculations. Each rate calculated by *SwimmingIndividuals.jl* is standardized to this modular temporal resolution. During each timestep, each individual makes behavioral decisions based on its own energy budget and functional type. There are currently five functional types within *SwimmingIndividuals.jl*: strong diel vertical migrators, weak diel vertical migrators, non-migrators, surface divers, and pelagic divers. Strong diel vertical migrants are species where all individuals in a population make daily vertical movements at dusk and dawn, and can resemble both standard diel vertical migration and reverse diel vertical migration. The depths at which an animal ascends or descends to is chosen from pseudo-randomly from a multi-modal distribution provided by the user for both day and night. Weak diel vertical migrants are species where on a proportion of individuals vertically migrate daily. The mechanism behind this individual movement is the same as strong migrants, but the decision to migrate or not is based on that individual’s gut fullness in a logistic function, where a near empty stomach will motivate the individual to migrant and a near full stomach will result in a greater likelihood of the individual remaining at their previous depth. Non-migrators do not make large vertical movements. Surface divers and pelagic divers make short dives into deeper waters to a random depth chosen (uniform distribution) between a minimum and maximum dive depth. The individual stays in the dive for a user-defined dive interval, ascends out of the dive, either to the surface (surface diver) or normal depth (pelagic diver) for a user-defined surface interval.

*SwimmingIndividuals.jl* relies on the calculation of an individual’s visual range, which could also be considered the individual’s perception range for non-visual sensory dynamics. The procedure closely follows work Aknses et al.5, which has been applied in other pelagic mechanistic modeling efforts6–8. The visual range hypothesis centers around the idea that animals have a limited world view, and the distance an animal can visualize (and make decisions based from) is a function of body size, visual acuity, the target’s (predator or prey) body size, and light irradiance. Light irradiance may change based on time of day, latitude, salinity, and season. Of particular importance is the decrease in light irradiance at depth, which is calculated in this model. *SwimmingIndividuals.jl* uses the body sizes of each focal individual and the visual range concept to restrict the predators and preys that an individual can perceive. Users should consider their study location when parameterizing *SwimmingIndividuals.jl* because the chosen environmental parameters directly influence predator-prey dynamics and energy budgets.

When the individuals are not actively migrating or diving, they make a decision to either eat or avoid predators. This decision is determined by a logistic function where an individual has a greater likelihood of eating when it is hungry and avoiding predators when it is full. Additionally, it is assumed that animals do not make feeding decisions while migrating or diving. In this way, animals make “riskier” decisions when approaching starvation. If the animal does not need to eat and there are no predators within their perceivable range, they randomly move on the longitude and latitude access according to ½ of the user defined swim speed (assumed to be cruising velocity). Vertical movement is not applied to the random movement because of the importance of vertical partitioning in pelagic ecosystems.9,10

Focal species predation is divided into sub-timesteps to ensure that individuals can consume multiple prey items per user-defined timestep, and still allow for the calculation of individual mortality for focal predation – focal prey predation events. Similar to the non-focal species, the density of focal and non-focal species is calculated, and the proportion is used to divide the feeding sub-timesteps so that individuals may consume both types of species. For predation of focal individuals, the distance between each potential prey (limited to 1%–10% of body size and within perceivable range) is calculated and the predator will predate the nearest prey. The predator then moves to the location of the prey, its’ stomach becomes fuller, the energy consumed is calculated, and the prey is removed from the simulation. Since non-focal species are organized as densities, rather than individuals, the individuals in each grid cell are assumed to be homogenously distributed (i.e., evenly spaced). The number of individuals consumed is determined from a Holling Type II functional response curve using the surrounding prey density, the perceivable range adjusted to the proportion of time remaining for non-focal predation, and a handling time (2 seconds default). The distance between each potential prey (assumed same for all preys) is used to calculate the time it will take an individual to travel to and consume the prey. Since all individuals are assumed to be the same distance from the predator, the predator chooses the available prey with the greatest energy density, so it maximizes its’ energy input. After predation, the amount of biomass and energy consumed is recorded and the non-focal species density within the appropriate grid cell decreases. This loop continues until time runs out, the predator has a full stomach, or there are no more preys.

The energy budget of each individual is adjusted according to the consumed energy, respiration rate, excretion rate, egestion rate, and specific dynamic action (energetic costs associated with digestion). The respiration rate is calculated as a function of temperature (location and depth-specific), body mass, and activity rate. A 1D depth-specific temperature has been implemented within *SwimmingIndividuals.jl* as a decay function from the surface (26C) to 3000m (4C), characteristic of the Northwest Atlantic Ocean. This temperature is currently considered the same for all latitude-longitude grid cells. The user should provide this information for their respective system by either changing the defaults in the “generate\_temperature()” function, or their own array expressing spatially explicit temperatures. The individual is considered active when the individual is diving, migrating, or feeding, and the energetic cost of respiration is adjusted according to a weighted average of active metabolic rates and standard metabolic rates11. Excretion and egestion rates are calculated as a function of consumed energy and a user-defined assimilation efficiency. The default assimilation efficiency is 80%12, which is also used as the default in other modeling systems, but can be easily adjusted by the user to match any discrepancies. This value means that 80% of the ingested energy is not egested. 80% of the remainder of this energy is then not excreted. Reducing the assimilation efficiency will result in a greater proportion of energy available in the individual’s energy reserves. The specific dynamic action (SDA) is calculated as 20% of the remaining energy. The change in an individual’s energy reserves is calculated as the difference of the ingested energy and the sum of all energy expenses (respiration, egestion, excretion, and SDA). Currently *SwimmingIndividuals.jl* does not convert excess energy into somatic fish growth or development of reproductive structures, as its current applications do not call for long-term assessments of population dynamics of focal species. The stomach fullness of an individual is reduced each timestep according to a temperature-dependent gut evacuation rate function13,14, which frees up space in the stomach to promote feeding in later timesteps. If an individual’s energy reserves reach 0J, the animal starves, is removed from the simulation, and mortality is applied to the species.

**Examples (I intend to add)**

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| --- | --- | --- |
| Example | *Parameters* | Code Location |
| AnimalMovements | 5 focal species; 1 ind. each; 1 day; 1 min. timestep |  |
| EnergyTrends | 5 focal species; 1000 ind. each; 1 year; 1 day output timestep; 20 min ind. timestep |  |
| PreyQuality | 10 focal species; 1000 ind. each; 1 year; 1 day output timestep; 20 min ind. |  |
| FoodWebs | 45 focal species; 100 ind. each; 1 year; 1 day output timestep; 30 min ind. timestep; all species replenish |  |

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**References**

1. Weisberg, S. J. *et al.* Merging trait‐based ecology and regime shift theory to anticipate community responses to warming. *Glob. Change Biol.* **30**, e17065 (2024).

2. Papastamatiou, Y. P. *et al.* Dynamic energy landscapes of predators and the implications for modifying prey risk. *Funct. Ecol.* (2023).

3. Brown, J. H., Gillooly, J. F., Alen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).

4. Wu, Z. & Forget, G. PlanktonIndividuals. jl: a GPU supported individual-based phytoplankton life cycle model. *J. Open Source Softw.* **7**, 4207 (2022).

5. Aksnes, D. L. Natural mortality, fecundity and development time in marine planktonic copepods-implications of behaviour. *Mar Ecol Prog Ser* **131**, 315–316 (1996).

6. Langbehn, T. J., Aksnes, D. L., Kaartvedt, S. & Fiksen, Ø. Light comfort zone in a mesopelagic fish emerges from adaptive behaviour along a latitudinal gradient. *Mar. Ecol. Prog. Ser.* **623**, 161–174 (2019).

7. Ljungström, G., Langbehn, T. & Jørgensen, C. Bergmann patterns in planktivorous fishes: A light‐size or zooplankton community‐size rule is just as valid explanation as the temperature‐size rule. *Glob. Ecol. Biogeogr.* (2023).

8. Ljungström, G., Langbehn, T. J. & Jørgensen, C. Light and energetics at seasonal extremes limit poleward range shifts. *Nat. Clim. Change* **11**, 530–536 (2021).

9. Angel, M. V. Biodiversity of the pelagic ocean. *Conserv. Biol.* **7**, 760–772 (1993).

10. Hopkins, T. L. & Gartner, J. V. Resource-partitioning and predation impact of a low-latitude myctophid community. *Mar. Biol.* **114**, 185–197 (1992).

11. Winberg, G. G. Rate of metabolism and food requirements of fish. *Fish. Res. Board Can.* **194**, 1–253 (1956).

12. Brett, J. & Groves, T. Physiological energetics: volume VIII, bioenergetics and growth. in *Fish Physiology* (eds. Hoar, W. S., Randall, D. J. & Brett, J. R.) 280–352 (Academic Press, 1979).

13. Pakhomov, E. A., Perissinotto, R. & McQuaid, C. D. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar. Ecol. Prog. Ser.* **134**, 1–14 (1996).

14. Hudson, J. M., Steinberg, D. K., Sutton, T. T., Graves, J. E. & Latour, R. J. Myctophid feeding ecology and carbon transport along the northern Mid-Atlantic Ridge. *Deep-Sea Res. Part Oceanogr. Res. Pap.* **93**, 104–116 (2014).