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ORIGINAL PAPER

Copepod foraging model finds efficient selection of small, high-quality prey patches using behavioral observations in *Acartia tonsa*

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Abstract

Phytoplankton vary both in their chemical compositions and distributions within marine environments. While zooplankton are known from lab settings to selectively eat chemically high-quality phytoplankton, it is highly challenging to directly observe these micro-interactions in nature. Here we develop a model to examine these interactions, testing whether copepods can effectively target high-quality prey. We used experimental data to parameterize a two-dimensional individual based model and simulated copepod movement through a prey field of uniform quantity, but variable quality. Copepods either displayed variable frequencies of behaviors depending on prey quality ('variable-behavior copepods'), or displayed the same frequency of behaviors, regardless of prey quality ('fixed-behavior copepods'). We examined: (1) the copepods' responses to the availability of high-quality, nitrogen-replete (HQ) food, (2) the copepods' responses to patch fragmentation, (3) the role of behavior in locating HQ food, and (4) how these factors combined to influence nitrogen ingestion throughout the day. Variable- and fixed-behavior copepods located HQ patches at the same speed, but variable-behavior copepods resided in HQ patches up to 1.8 times longer. Variable-behavior copepods ingested more nitrogen than fixed-behavior copepods. Based on our IBM, we suggest copepods can selectively utilize small patches of HQ food in the wild, and likely do so rapidly (<15 min). Future work should continue to model behavioral responses to prey quality to explore the link between ecological stoichiometry and behavioral ecology, and observed plankton distributions.

Keywords Individual based model (IBM) · Ecological stoichiometry · Selectivity · Marine · *Acartia tonsa* · Behavior

Introduction

Resources in nature are not equally distributed. Although this is well-accepted, this resource patchiness is not always immediately obvious, particularly in aquatic ecosystems where the dominant primary producers and consumers (phytoplankton and zooplankton) are microscopic (Shurin et al. 2006; Gruner et al. 2008; Macdonald and Johnson 2015). In their search for resources, aquatic organisms like zooplankton can sense differences in abiotic cues like light, nutrients, flow velocity, and salinity (e.g., Winder et al. 2003; Woodson et al. 2005, 2007; Stearns 1986), as well

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as biotic cues like the presence of food, predators, and conspecifics (e.g., Larsson 1997; Tiselius et al. 1997; Menden-Deuer and Grünbaum 2006). Consumers like copepods change how they forage depending on various biotic and abiotic signals, including environmental turbulence and prey motility (Saiz and Kiørboe 1995), and can actively search for prey using techniques like vertical migration (Herman et al. 1981). Additionally, zooplankton, including marine copepods, respond to environmental food concentration (Tiselius 1992; Leising and Franks 2002; Bochdansky and Bollens 2004), which can result in copepods forming large aggregations in areas of greater food abundance, both horizontally (Froneman et al. 1999; D'Ovidio et al. 2010) and vertically (Jaffe et al. 1998; Franks and Jaffe 2008). If these aggregations of copepods are large enough (centimeters to meters, or larger scales), they can be observed in the field using tools such as acoustic or video imaging (Jaffe et al. 1998; Lough and Broughton 2007), and can be correlated to phytoplankton abundance via fluorometry (Tiselius et al. 1994) or direct sampling near areas with elevated chlorophyll *a* (Herman et al. 1981). However, patches of phytoplankton and zooplankton that are smaller (millimeters to centimeters) are at biologically important scales, but are still very difficult to study using currently established techniques (Barth and Stone 2024).

While numerous studies have explored the importance of behavioral responses of aquatic consumers to heterogeneity in food quantity, our understanding of consumer responses to prey quality in situ are lacking. Laboratory experiments show that copepods sense and capture prey close to their mouthparts (Alcaraz et al. 1980) and then quickly accept or reject the captured material (Tiselius et al. 2013), presumably in response to factors including prey quality (Paffenhöfer and van Sant 1985; Poulet and Marsot 1978; Huntley et al. 1983; Herstoff et al. 2021; Meunier et al. 2016). One way of defining prey quality is via ecological stoichiometry, which considers the balance of elements in organisms (Sterner and Elser 2002). In aquatic ecosystems, phytoplankton quality, as characterized by its stoichiometry, may be heterogeneous in ways that do not map onto heterogeneity in phytoplankton abundance. Stoichiometric quality may vary due to relatively large-scale processes (from meters to kilometers, and hours to days), such as persistent oceanic fronts that create differential access to light or nutrients (Froneman et al. 1999; D'Ovidio et al. 2010), or differences in light availability throughout the water column (Sterner et al. 1997; Dickman et al. 2006). Alternatively, relatively small-scale processes (from centimeters to meters, and seconds to minutes) can also alter phytoplankton quality at scales relevant for copepods eating these phytoplankton. Phytoplankton respond to local nutrient enrichment from decaying, sinking aggregates (Stocker et al. 2008), or through excretion by consumers both large (Lavery et al. 2010; Roman et al. 2014) and small (Steinberg et al. 2002). Phytoplankton rapidly respond to changes in nutrient availability (Glibert and Goldman 1981; Goldman and Glibert 1982), and may alter their division rate (Myklestad 1977; Laws 2013) and engage in luxury uptake of nutrients (Elrifi and Turpin 1985). These responses can shift phytoplankton nutritional composition, resulting in variable quality at a range of scales (Verity et al.1992; Geider and La Roche 2002; Quigg et al. 2003; Finkel et al.2006).

This prey stoichiometric variation poses a challenge for marine zooplankton like copepods: while their phytoplankton prey can be stoichiometrically variable, particularly its carbon (C) and nitrogen (N) content (Sterner and Elser 2002; Frost et al. 2005; Meunier et al. 2014), consumers maintain relatively fixed internal stoichiometric ratios (Sterner and Elser 2002). Because even short-term exposure to poor-quality food can have deleterious consequences for copepod life-history (Malzahn and Boersma 2012), many copepods selectively consume stoichiometrically-advantageous prey from mixtures (Butler et al. 1989; Cowles et al. 1996; Meunier et al. 2016; Herstoff et al. 2021). Furthermore, copepods react to prey presence within seconds and begin feeding (Price et al. 1983), and can rapidly respond to differences in prey quality such as by altering their behavior (Herstoff et al. 2019). Herstoff et al. (2019) found that the behavioral responses of the copepod *Acartia tonsa* differed across life-history stage and with variations in food quality. Adults had the strongest responses to prey quality, decreasing their displacement and increasing the incidence of feeding behaviors when offered stoichiometrically-replete prey. Some responses depended on the quality of food during an extended preconditioning period prior to the behavioral trials. Consequently, Herstoff et al. (2019) suggested that use of high-quality food patches would be contingent on the size and persistence of such patches in the wild, and proposed that future work examine copepod foraging within a prey field of heterogeneous elemental stoichiometric content.

Because measurements of prey stoichiometry are relatively coarse compared to the small scales relevant to zooplankton (millimeters to centimeters), our knowledge of whether copepods might be able exploit heterogeneity in food quality is still very limited. Field-based methods to assess food quantity remain a relatively coarse process, and rely on analysis of relatively large samples that only reveal patterns in aggregate elemental or biochemical content (Twining et al. 2008), or use radioisotopic elemental tracers and flow cytometry to determine the rate at which phytoplankton incorporate nutrients (Lomas et al. 2010). Cell-specific methods that can produce much more detailed information about food quality are still too slow and labor-intensive to yield the needed spatial or temporal resolution

(Kreft et al. 2013). Thus, heterogeneity in prey quality could lead to patchiness that is important to consumers like copepods, but that remains undetectable by current measurement methods. While we know copepods respond to prey quality in complex ways in laboratory experiments (Herstoff et al. 2019, 2021), understanding the fine-scale responses of copepods in the field to differences in prey quality remains elusive. Modeling experiments, even if parameterized using relatively coarsely-gathered data on prey stoichiometry, offer an opportunity to increase our understanding of the small scales (millimeters to centimeters) at which differences in prey quality could be important to planktonic consumers.

Current models focus on zooplankton behavioral responses to food quantity (Leising and Franks 2000, 2002; Leising 2001, 2002), but not behavioral responses to food quality. For example, while a recent model included prey stoichiometry in an effort to understand structuring of copepod age classes and nutrient cycling within the ocean (Tanioka and Matsumoto 2018), variation in behavior in response to prey stoichiometry was not considered. In this study, we parameterized a two-dimensional (‘2D’) model using small-scale data on copepod behavior in response to prey quality to examine the spatial and temporal scales at which food quality may influence copepod foraging. A 2D model, while a simplification of real-life habitats, is computationally simpler and enables us to understand how behavior may allow copepods to utilize small-scale patches (millimeters to centimeters in size). The simulated environment had uniform prey abundance but variously sized patches of N-rich, high-quality ('HQ') food amongst an overall matrix of N-poor, low-quality ('LQ') food. Copepods performed three focal swimming behaviors using data gathered from experiments by Herstoff et al. (2019), and either varied their behavioral frequencies and speed in response to the quality of food encountered (‘variable-behavior copepods’), or their behavioral frequencies and speed were fixed to parameters associated with LQ prey, regardless of the true quality of food encountered (‘fixed-behavior copepods’). We examined: (1) the response of copepods to different availability of HQ food, (2) the response of copepods to food fragmentation, and (3) the role of behavior in locating HQ food. We used this information to examine (4) how these factors influenced the copepod’s daily ingestion of carbon (C) and nitrogen (N), and the resulting C: N ratio of ingested food, and hypothesize that the variable-behavior copepods should have a resulting food intake that is closer to their optimal ratio than those copepods that cannot change their behavior.

Table 1 Behavior probabilities for IBM

	Helical swimming	Linear movement	Wait
HQ	27.08 (3.46)	52.15 (3.71)	20.78 (3.55)
LQ	15.89 (3.23)	38.56 (4.27)	45.55 (5.76)

The mean probability of engaging in each of three behaviors (±1 SE) is listed with respect to high-quality (HQ) and low-quality (LQ) food. Data based on observations by Herstoff et al. (2019)

Materials and methods

Here, we briefly describe our individual-based model (‘IBM’) using an abbreviated version of the ODD protocol (‘Overview, Design Concepts, Details’, see Grimm et al. 2006). The full IBM description using the ODD protocol is available within Supplemental Material 1. We first *overview* information associated with the model. Next, we discuss strategic *design concepts* associated with the model. Last, we discuss technical *details* associated with IBM construction.

Overview

We used R Statistical Software (v4.3.1; R Core Team 2023; Maier 2022) to construct a 2-dimensional (‘2D’) IBM parameterized using data on behavioral responses of *Acartia tonsa* to food of different stoichiometric quality (Herstoff et al. 2019). We used a 2D model for several reasons. First, we had limited computational overhead, making coding and running three dimensional models challenging. Because we wanted explore many model scenarios, and because we did not want to limit the number of replicate simulated copepods in IBMs, we simplified our model by working in 2D space. Second, a 2D model captured helical swimming, a key behavior that almost always occurs in the X-Y plane (Herstoff et al. 2019). Lastly, we did employ three-dimensional (3D) IBMs using Julia programming language (Bezanson et al. 2017) for copepods with the same behavioral parameters as in our 2D models, where high-quality food took up 10%, 25%, or 50% of the volume of the 3D model; overall, the results matched our 2D IBMs findings (Supplemental Material 3). Because these 2D and 3D results matched, we chose to simplify our discussion of our model’s importance and focus solely on the 2D results.

In our IBM, simulated copepods could engage in one of three behaviors at each time step in the model: (1) helical swimming, which entails moving in a complete loop that starts/stops in the same spot, (2) displacing some distance and at some angle away from their current location, or (3) waiting at their current location and doing nothing. Based on high-speed video observations of *Acartia tonsa* gathered by Herstoff et al. (2019), we determined the probabilities of performing each of these behaviors in HQ and LQ food (Table 1).

To further prepare for running our IBM, we used data gathered on *A. tonsa* by Herstoff et al. (2019) to create separate databases containing information associated with the duration and displacement characteristics of each of these three behaviors in high-quality ('HQ') and low-quality ('LQ') food. These databases could be sampled with replacement, such that within a single time unit of the IBM (8 milliseconds, the length of time between two sequential frames of high-speed videos in Herstoff et al. (2019), simulated copepods would either perform linear displacement and move to a new location, some angle and distance away, or would wait at their current location for some multiple of this time unit, if performing waiting or helical swimming.

Helical swimming was particularly important because >90% of feeding occurs during this behavior (Henriksen et al. 2007). Thus, we assumed that only copepods performing helical swimming were consuming prey, and ingested food of the quality where the behavior was initiated. Copepods performing linear displacement or waiting were assumed not to eat. Copepods performing linear displacement moved away from their starting location at a simplified series of angles (Table 2); a visual check of linear displacement patterns showed that, overall, simulated copepods reached all areas of the simulated environment.

Simulated copepods either (1) varied the frequency and speed at which they engaged in the three focal behaviors in response to food quality at their current location ('variable-behavior copepods'), or (2) responded to HQ and LQ food with a fixed set of behavioral frequencies and speeds, parameterized using data associated with LQ prey, regardless of the true food quality at their current location ('fixed-behavior copepods').

The simulated environment was a square with edge lengths of 500, 1000, or 5000 mm (respectively, 'small-', 'medium-', and 'large-grained environments') (Fig. 1A). Because adult *A. tonsa* is ~1 mm long, distances in the simulated environment corresponded with distances as measured in copepod body-lengths. All simulated environments had wrapping edges; individuals encountering an edge proceeded through that edge and reappeared at the same location on the opposite side of the environment before finishing their movement (Fig. 1B). Wrapping edges essentially expand the IBM's scale by making it an infinite series of identical environments tiled throughout space (Fig. 1C). Thus, the frequency at which these environments repeated over space increased with decreasing length of the edges. These different edge lengths therefore allowed us to separately explore how the grain size (=fragmentation of HQ habitat) affected the copepod's ability to locate and reside within HQ patches, independently of HQ food availability.

Table 2 The probability of moving at each angle in high-quality (HQ) and low-quality (LQ) food

Angle	HQ	LQ
0°	52.14	60.82
18°	3.97	3.25
54°	4.28	2.50
90°	4.65	2.34
126°	3.84	2.12
162°	3.72	3.71
198°	8.31	7.79
234°	4.15	3.93
270°	6.94	6.43
306°	4.46	3.86
342°	3.53	3.25

Probabilities are listed as percent of movements at each focal angle in HQ or LQ food. Movements were categorized as straight swimming (0°), and as the midpoints of ten equally-spaced angles from >0° to <360°. Data based on observations by Herstoff et al. (2019)

While the IBM always contained the same concentration of non-depleteable food throughout the simulated environment, our treatments varied the percentage of the simulated environment containing HQ food (Table 3). HQ food existed in a single patch in the IBM and was surrounded by LQ food (Fig. 1A). In the lowest availability treatment, 0.77% of the environment space contained HQ food. This percentage was progressively doubled until 50% of the environment contained HQ food (Table 3).

The IBM process is overviewed in Fig. 2, and associated R code is available in Supplementary Material 2. In brief, to run the IBM, a single simulated copepod was seeded to a random X-Y location within the simulated environment. The simulated copepod assessed whether it was at a location with HQ or LQ food. A random number from 0 to 1 was generated. That random number, information about the current location's food quality, and the copepod's assignment to have variable- or fixed-behavior, were all used to determine the probability of the individual: (1) performing helical swimming for some number of time units, (2) moving linearly for some distance and at some angle from its current location within a single time unit, or (3) waiting at its current location for some number of time units (Table 1). A counter in the IBM recorded the X-Y location where the behavior was initiated, whether that location contained HQ or LQ food, and the behavior performed at each time step. This process was repeated with 1000 individuals, one by one, each moving for 1×10^5 time steps (=800 s, or 13.33 min).

Design concepts

From the IBM's digital counter, we determined the percentage of time individuals spent in locations containing HQ and LQ food, and the frequency of each of the three focal behaviors. Because we assumed that helical swimming was a proxy for feeding, we used information gathered for the number and duration of helices performed in HQ and LQ

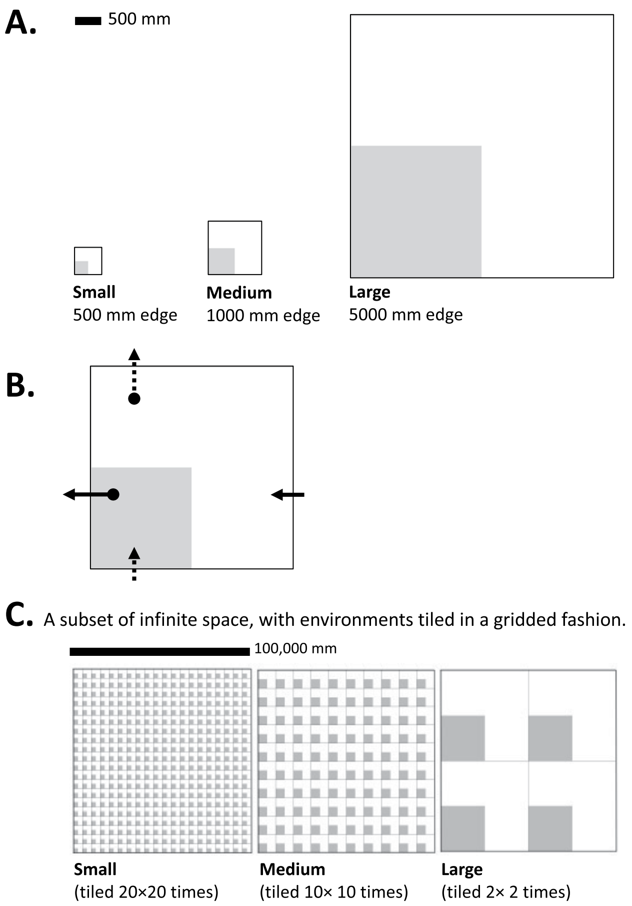

Fig. 1 An illustration of the simulated environments. This figure's purpose is to illustrate how different sized environments, filled with the same percentages of high-quality (HQ) and low-quality (LQ) food, resulted in different distances the simulated copepods had to travel before encountering the next area with HQ prey. This setup allowed us to study the importance of both food fragmentation and behavioral responses to food quality for simulated copepods locating and residing within areas with HQ food. Throughout this figure, each simulated environment shown has 25% HQ food (grey space) and 75% LQ food (white space). **(A)** Simulated environments are shown as either small, medium, or large squares, with edges 500, 1000, or 5000 mm long, respectively. Because the body length of an adult *A. tonsa* is ~1 mm, the environment's edges were 500, 1000, or 5000 body-lengths long. We refer to environments with these different edge lengths as small-, medium-, and large-grained, respectively. **(B)** The simulated environments had wrapping edges to prevent edge effects. For example, during linear displacement, a simulated copepod swims from its current location, indicated by the black point at the left edge of its current environment, into a corresponding location on the right edge of a new, identical environment (solid arrows). Similar logic applies to the top and bottom edges of the simulated environment (dashed arrows), and for movement in opposite directions. **(C)** Because of the environment's wrapping edges, the IBM provided simulated copepods an infinite series of identical environments repeated through space in a gridded fashion. This illustration shows a subset of this infinite space as a square with edges 100,000 mm long, wherein the small-, medium-, and large-grained environments are displayed in a 20×20, 10×10, and 2×2 grid. Because of the coarseness of the environment as a whole relative to the size of the simulated copepod, and because relative amount of HQ food differed between the various IBM simulations, the simulated copepod traveled different distances within and between the gridded environments to encounter a patch of HQ food.

Table 3 The availability of high-quality (HQ) food in environments of different grain sizes.

% HQ	Small	Medium	Large
50	354	707	3536
25	250	500	2500
12.50	177	354	1768
6.25	125	250	1250
3.13	88	177	885
1.56	62	125	624
0.77	44	88	439

The left column shows the percentage of the simulated environment filled with HQ food. The grain size of the environment was small, medium, or large (squares with 500, 1000, or 5000 mm edges, respectively; see Fig. 1A). HQ patches were square spaces with edges of the listed length, in mm. The remainder of the environment was filled with low-quality (LQ) food.

food to calculate the simulated copepod's daily ingestion of C, N, and the resulting C: N intake.

Individuals were assumed to immediately sense and respond to food quality only at their current location, and did not retain a 'memory' of food conditions in previous time steps or locations. Therefore, behaviors were simply based on a random number drawn and compared to probabilities (Tables 1 and 2) based observed experimental behavior (Herstoff et al. 2019) While this may oversimplify the ability of copepods to respond to prey quality (Augustin and Boersma 2006) and overlooks the ability of copepods to potentially sense more distant prey (e.g., Strickler 1982; but see Gonçalves and Kiørboe 2015), our model still useful as it is a first attempt to determine the spatial and temporal scales at which heterogeneity in food quality influences copepod behavior and foraging.

Details

To examine copepod foraging in response to heterogeneous prey quality, we altered various IBM parameters to create a series of submodels examining our four focal questions.

The importance of HQ food availability

We examined the effect of variable HQ food availability (i.e., patch size) on a simulated copepod's location of, and residency within, HQ patches. HQ food took up different percentages of space within the simulated environment (Table 3), and the individual's behaviors varied depending on food quality (Table 1).

The importance of patch fragmentation

We examined the effect of variable environment grains (i.e., patch fragmentation) on a simulated copepod's ability to locate and stay within HQ patches. Grain size varied (small,

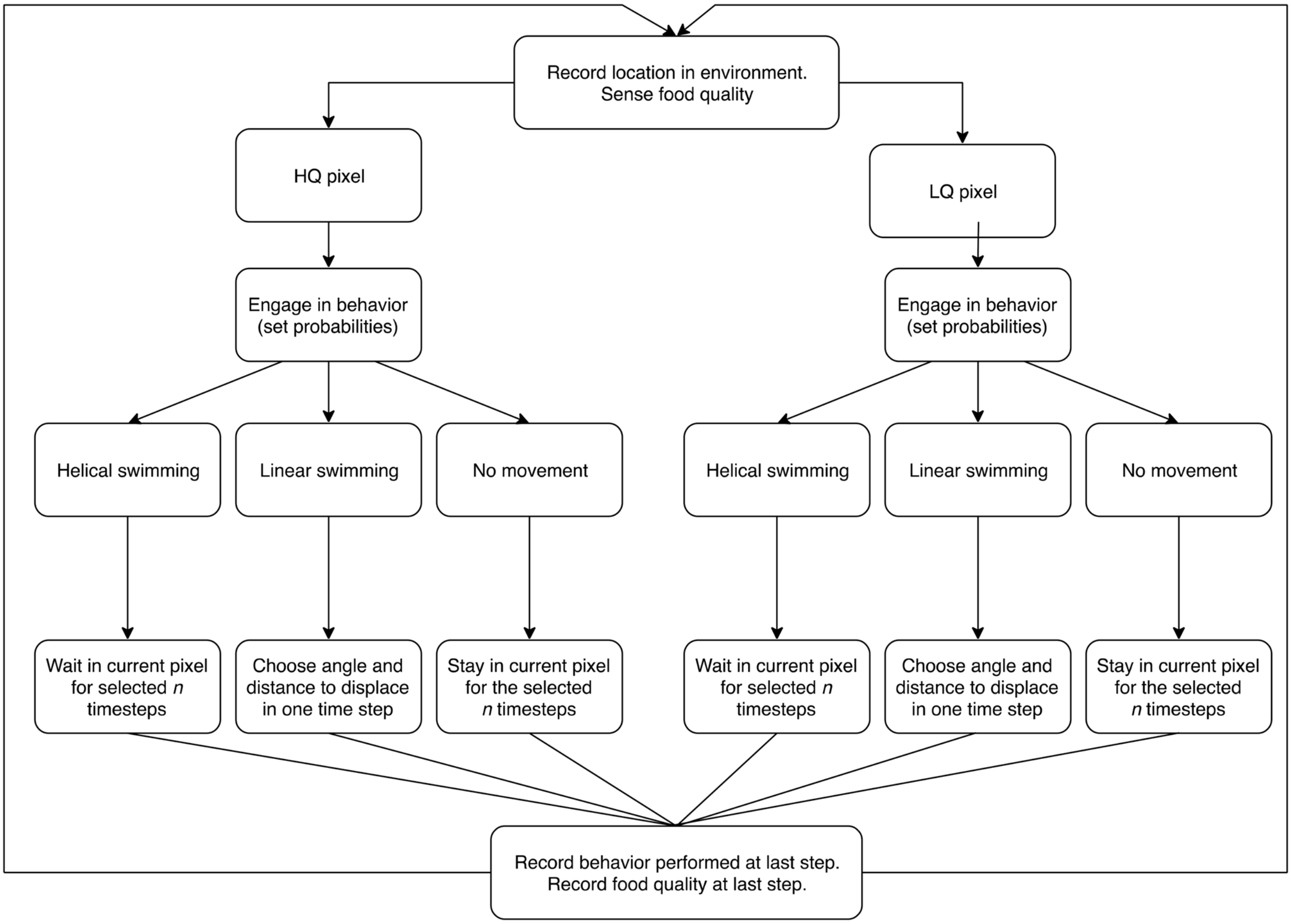

Fig. 2 Scheduling overview for IBM

medium, and large), and contained different availabilities of HQ food (Table 3) which were distributed at different distances from each other (e.g., Fig. 1C), allowing us to assess the importance of patch fragmentation. Behaviors of the individuals varied depending on food quality (Table 1).

The importance of behavior in locating HQ food

We compared variable-behavior copepods, whose behavioral frequencies and speed varied depending on whether their location contained HQ or LQ prey (Table 1), to fixed-behavior copepods, whose behavioral frequencies and speed were fixed to parameters associated with LQ prey, regardless of the food's true quality (Table 1).

Estimating daily C: N intake

We examined how behavior, patch size, and patch fragmentation influenced a copepod's daily acquisition of C, N, and their overall C:N intake. Based on calculations using data from Herstoff et al. (2019) and Augustin and Boersma (2006), we suggest that large differences in the amount of time spent helical swimming resulted in similar cell ingestion rates copepod^{-1} hour^{-1}, but variable elemental intake per unit time. Element consumption was estimated by applying measurements of copepod ingestion rates (Augustin and Boersma 2006) to prey used to parameterize experiments (Herstoff et al. 2019). Next, we determined the fraction of time copepods were engaged in helical swimming in HQ and LQ patches. We combined this information to calculate ingestion rate in moles of C or N consumed copepod^{-1} hour^{-1}, which was converted to dietary C:N. This was compared to 7.12, the predicted optimal C:N threshold elemental ratio for *Acartia tonsa* (Anderson et al. 2017).

Results

We performed two tests to check IBM outputs. First, 'fixed-behavior' copepods in our simulations were parameterized using data for LQ behavioral responses (Table 1). We examined the effect of parameterizing fixed-behavior copepods using LQ *versus* HQ data, and found that the models produced very similar responses (Supp. Table 1). Thus, we used LQ data to parameterize fixed-behavior copepods in our simulations. Second, we examined the null expectation that the residency and behavior for fixed-behavior copepods would closely match the proportion of the simulated environment containing HQ food (e.g., in models with 25% HQ, a null expectation of 25% residency in HQ patches by fixed-behavior copepods). We found a close match between the null expectation and model outputs based on the availability of HQ food; these outputs were noticeably different when compared against variable-behavior copepods (Fig. 3; Table 4). Further descriptions of both test results are available in Supplemental Material 3.

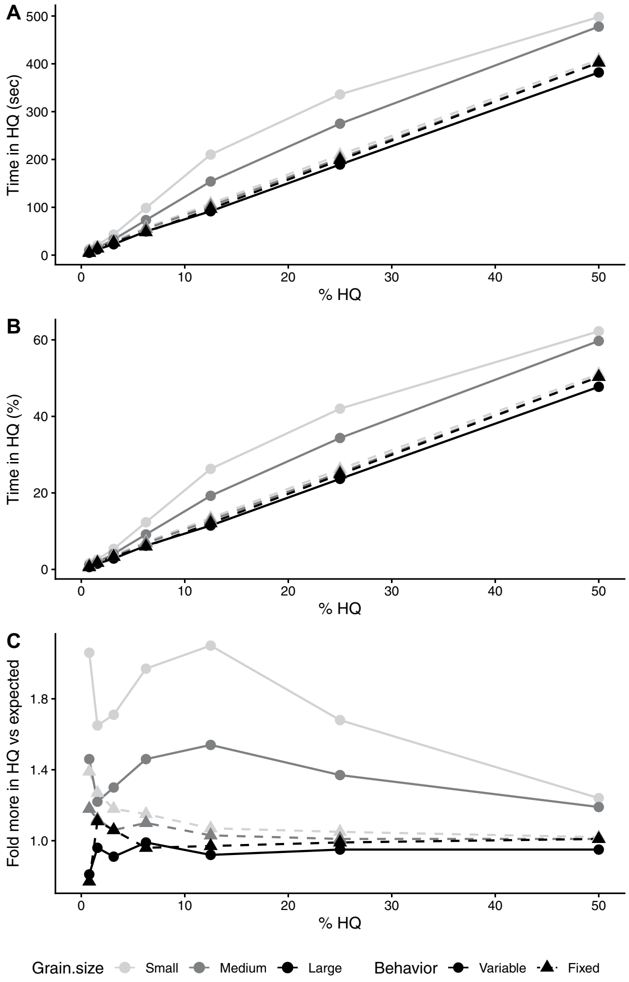

Fig. 3 Mean residence in high-quality food patches in response to availability of high-quality (HQ) food. In all panels, the percentage of the model space filled with high quality food (% HQ) is shown on the bottom axis. Note that the different panels have varying scales on the y-axis. For all panels, Grain size, indicated by point colors, varied from small, to medium, to large (light, medium, and dark grey, respectively). Simulated copepods either had variable-behavior, and altered their speed and behavioral frequency in response to food quality (circular points, solid lines), or had fixed-behavior, and displayed speeds and behavioral frequencies associated with LQ prey, regardless of food quality encountered within the simulated environment (triangular points, dashed lines). **(A)** Mean time (in seconds) in HQ food. Total run time of the IBM was 800 s (=13.33 min). **(B)** Mean time (as a percent of the total run time) in HQ food. **(C)** The fold-more time in HQ food versus expected. For example, a simulated copepod in a model with 12.5% HQ food available was expected to spend 12.5% of its time in HQ patches. A table of the values used to create this figure is available in Supplemental Material 4.

For variable-behavior copepods, whose behavior frequency depended on food quality, residency in HQ patches was most different from the null expectation when the grain size was small or medium (Fig. 3). For example, in the small-grained environment, copepods spent an average of 42.01% of their time in HQ patches when these patches accounted for only 25% of the simulated environment space, or1.68-fold more time than the null expectation of 25%. In the same scenario with medium grained environments, variable-behavior copepods spent an average of 34.35% of their time in HQ patches, or 1.37-fold more time than the null expectation (Fig. 3B). However, the advantage of variable-behavior diminished when patch grain was larger. In the same scenario with large-grained environments, variable-behavior copepods spent an average of 23.67% of their time in HQ patches, close to null models containing 25% HQ food (Fig. 3B).

Varying behavior in response to food quality had the greatest effect on residence time in HQ patches when HQ food made up 12.5% or less of the simulated environment. Where HQ food was more abundant, the advantage of variable-behavior was relatively smaller (Fig. 3). For example, for variable-behavior copepods in small-grained environments that contained 0.77% HQ food, we observed 1.58% residency in HQ patches, representing 2.06-fold more time in HQ patches compared to the null expectation. When 50% of the space contained HQ food, variable-behavior copepods resided 62.24% in HQ patches, representing only 1.24-fold more time in HQ patches compared to the null expectation (Fig. 3C).

The patterns of time spent helical swimming in HQ patches were qualitatively similar but more pronounced than patterns of residence time in HQ patches (Fig. 4). Because real copepods performed 1.69 times more helices in HQ food than LQ food (Table 1; based on Herstoff et al. 2019), variable-behavior copepods engaged in helical swimming for more time than fixed-behavior copepods (Fig. 4). Simulated copepods with variable-behavior spent ~2–3 times longer performing this important feeding-associated behavior compared to fixed-behavior copepods. Grain of the simulated environment affected time spent in helical swimming. For example, in small-, medium-, and large-grained environments with 25% HQ food, helical swimming was performed for an average of 233.86, 191.28, and 131.85 s by variable-behavior copepods, respectively, compared to 67.57, 65.35, and 64.16 s by fixed-behavior copepods during the IBM (Table 4). As helical swimming is closely linked to feeding (Henriksen et al. 2007), this led to

Table 4 Comparison of time performing helices between variable- and fixed-behavior copepods.

Grain size	% HQ	Variable-behavior copepods		Fixed-behavior copepods		
		Time (sec) helical swimming in HQ (Fig. 4)	% Time budget in HQ	Time (sec) helical swimming in HQ (Fig. 4)	% Time budget in HQ	Variable: Fixed ratio time budgets
Small	50	346.55	43.32	131.65	16.46	2.63
	25	233.86	29.23	67.57	8.45	3.46
	12.5	146.29	18.29	34.58	4.32	4.23
	6.25	68.61	8.58	18.46	2.31	3.72
	3.13	29.81	3.73	9.50	1.19	3.14
	1.56	14.33	1.79	5.12	0.64	2.80
	0.77	8.81	1.10	2.77	0.35	3.18
Medium	50	332.49	41.56	129.74	16.22	2.56
	25	191.28	23.91	65.35	8.17	2.93
	12.5	107.18	13.40	33.08	4.14	3.24
	6.25	50.94	6.37	17.69	2.21	2.88
	3.13	22.70	2.84	8.51	1.06	2.67
	1.56	10.61	1.33	4.52	0.57	2.35
	0.77	6.27	0.78	2.35	0.29	2.67
Large	50	265.66	33.21	129.78	16.22	2.05
	25	131.85	16.48	64.16	8.02	2.06
	12.5	63.83	7.98	31.19	3.90	2.05
	6.25	34.52	4.32	15.46	1.93	2.23
	3.13	15.79	1.97	8.54	1.07	1.85
	1.56	8.33	1.04	4.46	0.56	1.87
	0.77	3.45	0.43	1.52	0.19	2.26

Variable-behavior copepods varied their speed and behavioral frequencies in response to food quality encountered; fixed-behavior copepods responded to food with the behavioral frequencies and speeds associated with LQ prey, regardless of food quality within the simulated environment. Helical swimming in HQ patches shown, both as mean time (in seconds; Fig. 4), and as mean percentage of the copepod's time budget spent performing helical swimming in HQ (out of 800 total seconds). Time helical swimming shown for variable and fixed-behavior copepods, with respect to the various simulated environment's grain size ('Grain size') and HQ food availabilities tested ('%HQ'). The last column shows the ratio of the time budgets, where variable copepod budgets were divided by corresponding fixed copepod budgets.

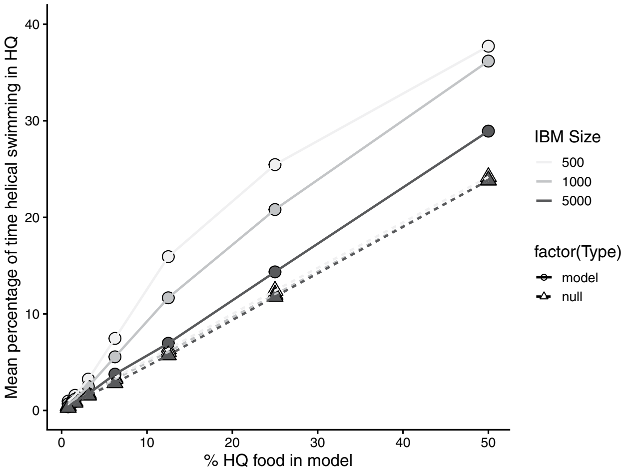

Fig. 4 Mean percent time performing helices in HQ patches in response to availability of high-quality (HQ) food. Grain size and copepod behaviors as indicated by inset key, and described in the legend of Fig. 3

large differences in percentages of time spent feeding within HQ food patches. For example, where 25% of the environment contained HQ prey, variable-behavior copepods spent 29.23%, 23.91%, and 16.48% of their time budget in HQ food in small-, medium-, and large-grained environments, respectively, compared to fixed-behavior copepods that spent 8.45%, 8.17%, and 8.02% of their time budget in HQ food in the same environments (Table 4). Like the patterns described for mean residence time, there was an increasingly greater relative advantage of variable-behavior where HQ food was rarer, particularly in smaller-sized environments (Table 4; Figs. 3 and 4).

A copepod's ability to vary its behavior in response to food quality did not affect the average length of time needed to first locate an HQ patch–i.e., variable- and fixed-behavior copepods found HQ patches at similar rates (Fig. 5). However, both larger-proportion of space with HQ patches and smaller-grained environments allowed copepods to more rapidly locate HQ patches (Fig. 5A). The latter pattern was due to the decreased distance individuals had to travel to

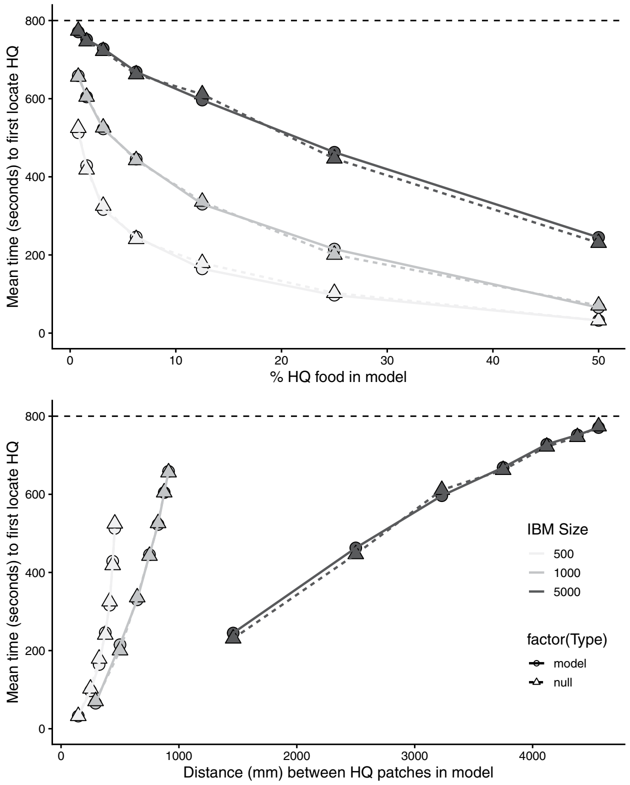

Fig. 5 Mean time to first locate high-quality (HQ) food in response to availability of HQ food. Data is shown as time to first locate HQ patches with respect to (**A**) the percentage of the simulated environment with HQ food, or (**B**) the distance between HQ patches in the simulated environment. The dashed horizontal line represents the total IBM run time of 800 s. Grain size and copepod behaviors as indicated by inset key, and described in the legend of Fig. 3

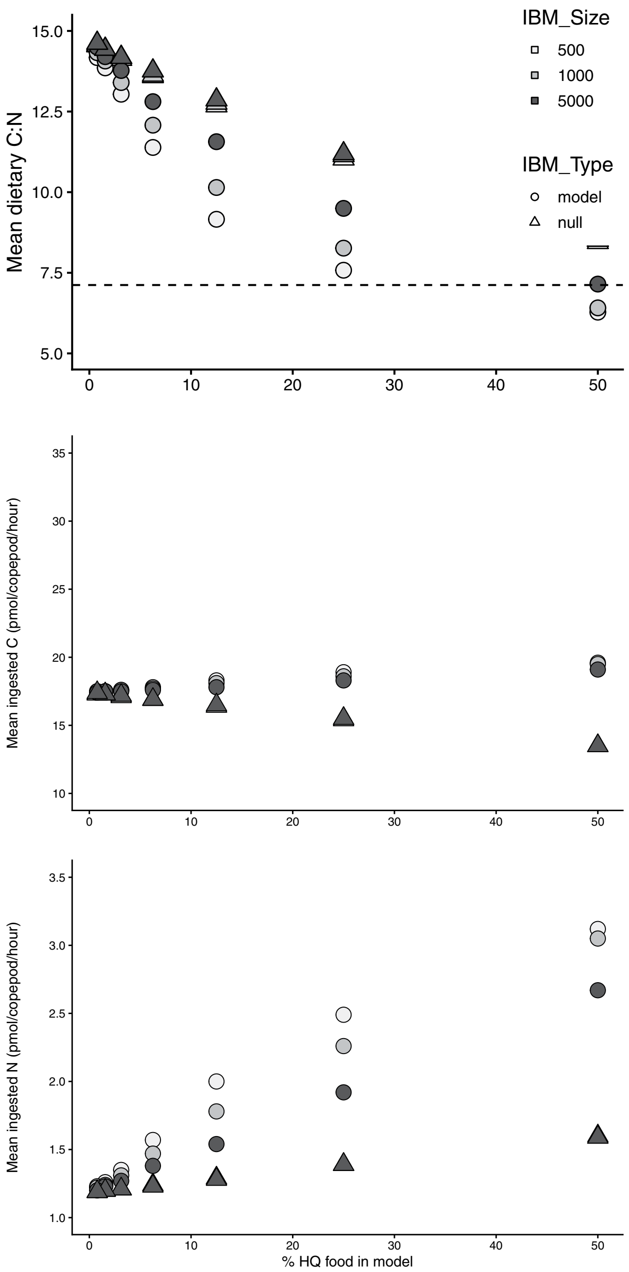

Fig. 6 Estimated daily elemental consumption in response to availability of high-quality (HQ) food. Grain size and copepod behaviors as indicated by inset key, and described in the legend of Fig. 3. (**A**) Mean C:N in a simulated copepod's diet. The dashed horizontal line represents the predicted optimal threshold elemental ratio for *Acartia tonsa* of 7.12 C:N (Anderson et al. 2017). (**B**, **C**) Mean C and N ingested per simulated copepod per hour

encounter the next area with HQ food in smaller grained environments (Fig. 5B).

Copepods that varied ingestion rate in response to food quality always had a lower average dietary C:N and higher C and N ingestion rates than did copepods with fixed-behavior (Fig. 6). Carbon and nitrogen ingestion rates differed most between the variable- and fixed-behavior copepods at the highest proportion of HQ food, being 45.19%, 44.44%, and 41.48% higher for variable-behavior copepods ingesting C in small, medium, and large-grained environments, and 95.00%, 91.82%, and 67.92% higher for variable-behavior copepods ingesting N in small, medium, and large-grained environments, respectively (Fig. 6B, C). The dietary C:N ratios of both variable- and fixed-behavior copepods declined with increasing proportions of HQ food as expected, but never reached the optimal value of 7.12 (Anderson et al. 2017; Herstoff et al. 2021) for the fixed-behavior copepods, whereas the variable-behavior copepods reached this dietary C:N when 50% of the environment consisted of HQ food (Fig. 6A). The absolute difference in dietary C:N ratios between variable- and fixed-behavior copepods was greatest when 12.5% and 25% of the environment consisted of HQ food patches (Fig. 6A). Dietary C:N was lowest for the variable-behavior copepods in smaller-grained environments, with these differences being largest in absolute terms when HQ food constituted between 6.5% and 25% of the environment (Fig. 6A).

Discussion

We currently lack the ability to detect variation in prey quality in situ at small scales (millimeters to centimeters) relevant to zooplankton, but models allow us to leverage experimental evidence to explore the scales at which differences in prey quality may be important for consumers like copepods, and whether behavior may allow consumers to better target high-quality prey. Our IBM is the first to examine how behavioral responses to variations in prey stoichiometry may influence copepod distributions, feeding, and ultimately, C:N ingestion. We utilized a 2D model because it required less computational overhead, and because the key feeding behavior of *A. tonsa* could easily be modeled in two dimensions. Our use of a 2D model aligns with previous models that study of zooplankton behavior (e.g., Leising 2001, 2002; Leising and Franks 2000; Batchelder et al. 2002). Although our 2D model certainly oversimplifies the three-dimensional world copepods inhabit, it allowed us to explore a world of small-scale patches of varying food quality—a world we know exists, yet we cannot yet explore in real-time. Additionally, we found that our 2D model results matched our findings for our limited runs in 3D model space (Supplemental Material 3). Therefore, our model represents an important step in exploring the role of behavior of behavior for utilizing small, ephemeral patches of high-quality food. Our IBM's results emphasized the importance of copepod behavior in maximizing the animal's ingestion of high-quality food, particularly when patches were relatively small and fragmented (~500 mm). Variable-behavior copepods, whose behavioral frequency and speed varied in response to food quality, increased their residency in HQ patches and ingested a more N-rich diet with lower C:N relative to fixed-behavior copepods, whose behavioral frequencies and speed did not vary in response to food quality. Because phytoplankton elemental content is likely heterogeneous across different spatial and temporal scales (Verity Peter et al. 1992; Geider and La Roche 2002; Quigg et al. 2003; Finkel et al. 2006), our results highlight the importance of behavioral responses to food quality, and indicate that certain environmental conditions may allow copepods to rapidly exploit small patches of HQ food.

Currently, most models do not consider prey stoichiometry explicitly, and do not consider its consequences for the grazer (Flynn 2005; Mitra et al. 2014; but see Sailley et al. 2014; Tanioka and Matsumoto 2018). Where models do include copepod selectivity based on prey stoichiometry, they suggest prey stoichiometry could help explain seasonal plankton dynamics (Sailley et al. 2014), particularly across consumer ontogeny (Tanioka and Matsumoto 2018). Because copepods respond rapidly to prey presence (Price et al. 1983), and because food quality influences copepod prey selection (Cowles et al. 1988; Butler et al. 1989; Meunier et al. 2016; Herstoff et al. 2021) and behavior (Herstoff et al. 2019), our IBM suggests that both consumer selectivity and rapid behavioral responses to small, high-quality prey patches may be important to incorporate into ecosystem and food web models.

Varying behavior in response to food quality allowed copepods to reside longer in HQ patches, particularly if those patches were relatively small, relatively close together, and the simulated environment contained <25% HQ prey. This suggests copepods may accumulate in small HQ prey patches, on the order of 1.94–125.32 m^2 in size. Such small-scale variation in prey stoichiometric content is expected to exist; phytoplankton rapidly respond to nutrient enrichment (Myklestad 1977; Elrifi and Turpin 1985; Laws 2013) and alter their nutrient content in the order of minutes (Glibert and Goldman 1981; Goldman and Glibert 1982). However, such small-scale variation in prey quality is not yet detectable in situ with current methods. Thus, while small, fragmented, HQ prey patches are unlikely to persist for long periods within the ocean, our IBM suggests these small patches may be used effectively by copepods in nature. Because copepods can respond rapidly to food (Price et al. 1983; Tiselius 1992; Paffenhöfer and van Sant 1985; Tiselius et al. 2013), and because even short-term exposure to poor-quality food can be deleterious to copepod life-history history (Malzahn and Boersma 2012), it is to the copepod's advantage to be able to sense and rapidly change their behavior to exploit these small, HQ prey patches. However, in nature, these small patches quickly dissipate through turbulent diffusion; within active, turbulent shear mixing layers, patches dissipate at 10^{-8} to 10^{-5} $m^2 s^{-3}$ (Mullin 1963; Richman and Rogers 1969; Hansen et al. 1994). Furthermore, turbulence can also influence copepod foraging behaviors (Saiz and Kiørboe 1995). Future work should build three-dimensional models that incorporate turbulence and the diffusion rate of materials, as well as variation in copepod behavior in response to water conditions, to understand whether copepods would actually be able to take advantage of small, ephemeral patches in real-world environments. Additional work should also incorporate information on remote sensing of patches, such as via scent (e.g., Strickler 1982; but see Gonçalves and Kiørboe 2015), to determine if directional swimming based on prey chemical cues may further allow some species of copepods to target HQ prey patches. Lastly, future work should also consider building a model where both quality and quantity of food co-vary, as we know from laboratory experiments and empirical data that both food quality (Malzahn and Boersma 2012; Meunier et al. 2016) and quantity (Guisande and Harris 1995; Guisande et al. 1996) influence copepod growth and reproductive success, and factors like food quantity can determine copepod distributions in the field (Paffenhöfer and Stearns 1988). Overall, our model simplified conditions to study if *A. tonsa*'s behavior in response to variable food quality (but uniform quantity) influenced its ability to exploit small, high-quality patches. Although our setup simplifies how resources are distributed in space by using homogeneous and evenly-spaced patches, we anticipate that increasing model complexity by including diffusing patches of the same grain size would be an interesting comparator to study the importance of patch quality. We predict that this new model with diffusing patches would produce similar overall patterns to our current model, but with greater variance in results. Such a finding would further enforce our findings of the importance of copepod behavior in response to variable food quality. We predict that the patchiness of food quantity and quality that exists in nature creates strong evolutionary pressure for consumers like copepods to evolve behaviors that increase their sensitivity to prey characteristics, and can ultimately result in patchy distributions of predators and prey, and variation in the predator's biological success.

In our simulations, the average daily C:N ingested was greater than the optimal threshold elemental ratio of 7.12 C:N for *Acartia tonsa* (Anderson et al. 2017), except for variable-behavior copepods in small- and medium-grained environments that contained 50% HQ prey. In our IBM, the dietary C:N of all simulated copepods was closest to this optimal threshold elemental ratio when 50% of the environment contained HQ food, and copepods ingested a mixture of both HQ prey that was relatively N-rich, and LQ prey that was relatively N-poor, and altered their ingestion rate in response to prey quality. As N-rich, HQ prey became scarcer, all simulated copepods whose ingestion rates varied with prey quality consumed a diet that was too N-poor. However, variable-behavior copepods ingested diets that were, on average, closer to their optimal threshold elemental ratio as compared to fixed-behavior copepods, especially at intermediate percentages of HQ food in the environment.

Responding to prey quality both by altering ingestion rate and by altering behavior allowed dietary 'mixing and matching' of prey of different stoichiometric quality. This allowed simulated copepods to ingest a diet with an intermediate C:N that more closely matched their optimal threshold elemental ratio, as compared to simulated copepods whose ingestion rate was fixed to be the same, regardless of food quality. Indeed, *Acartia tonsa* have been demonstrated to alter their ingestion patterns in response to prey quality, so as to 'mix and match' prey of varying C:N and achieve a diet with an intermediate C:N that matches the copepod's optimal threshold elemental ratio of 7.12 C:N (Herstoff et al. 2021). Thus, we consider our IBM a simple but useful illustration of how changing behavior and ingestion rate in response to prey quality may help real copepods achieve their optimal threshold elemental ratio.

One caveat of our model is that copepods could only engage in a simple suite of three behaviors. In reality, we expect that real copepods engage in a complex suite of behaviors, which may allow copepods to respond even more precisely to variations in prey quality as encountered in prey patches and thus helps the copepod meet its optimal threshold ratio by altering its feeding patterns. Indeed, a recent study demonstrated that live copepods in experiments can select between food that simultaneously varies in numerous traits to obtain a C:N matching their threshold elemental ratio (Herstoff et al. 2021). More empirical work should explore how the full behavioral suite of copepods influences their ability to forage in nature and use this to parameterize models. Because copepods are a key link between microscopic and macroscopic consumers in marine food webs (Lavigne 2003), and because their selective feeding could determine elemental ratios in recycled, suspended, and sinking material, and, thereby influence biogeochemical rates (e.g., Elser et al. 1996; Steinberg et al. 2002; Meunier et al. 2016; Franco-Santos et al. 2018), future ecosystem models should incorporate copepod behavior and selectivity in a to better understand their potential to drive ecological stoichiometry and observed plankton distributions in marine habitats.

Another caveat of our model is that it was parameterized using observations of adult individuals of the calanoid copepod *Acartia tonsa*. Future work should consider modeling other copepod species that spend less time waiting to determine the importance of behavior. In HQ patches, ~21% of the modeled *A. tonsa*'s time budget was spent not moving, and this percentage was more than doubled in LQ patches. Other copepod species are much more active than *A. tonsa*. For example, another calanoid copepod species, *Clausocalanus furcatus*, spends 73–100% of its time actively swimming (Uttieri et al. 2008). Species like *C. furcatus* that employ more active behavior have different prey encounter patterns than copepod species that spend more time waiting and/or sinking (Uttieri et al. 2010). Such active copepods, which may spend more time feeding while on the move as compared to *A. tonsa*, which was assumed to only feed during helical swimming, may have different patterns of residence time within HQ patches, and ultimately, different daily C:N ingestion rates. Other important differences between copepods may also influence results; for example, different copepod species and/or life stages have different behaviors and elemental requirements (Herstoff et al. 2023), or differ in important behaviors like prey capture methods (Saiz and Kiørboe 1995; Paffenhöfer and van Sant 1985) or the use of vertical migration related to foraging (Stearns 1986; Herman et al. 1981). Gathering more empirical data on different copepod species and/or life stages and using this to parameterize an IBM could produce interesting results, as perhaps the ability to vary behavior in response to food quality may differ in importance depending on different depending on the copepod are considered.

In conclusion, our IBM is a first attempt to explore how behavioral responses to variations in prey stoichiometry influence patterns of predator distribution, feeding, and ultimately, C:N ingestion rates, in response to the size and distribution of prey patches of varying quality. The simulated copepods in our IBM effectively utilized small patches of HQ food on relatively short time scales. Our results suggest that including both consumer selectivity and behavioral responses to small, high-quality prey patches may be important to incorporate into ecosystem and food web models.

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Author contributions EMH collected the data on copepod behavior used to parameterize the model with CLM and MB. EMH and MU designed and coded the model in R. EMH wrote the first draft of the manuscript, which was improved by all authors.

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Data/code availability Code and data are available in Supplementary Material 1.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethics approval The authors declare no ethical approval was needed.

Statement of significance Prey quality varies substantially in aquatic ecosystems, even at small scales. Behavioral responses to differences in prey quality could influence the distribution and dietary stoichiometry of important consumers, like marine copepods, and their prey. However, we currently cannot study this in situ. Our paper is the first to develop a two-dimensional individual based model (IBM) to explore how behavioral responses to differences in prey quality influence (1) the copepod's responses to the availability of high-quality, nitrogen-replete (HQ) food, (2) the copepod's responses to patch fragmentation, (3) the role of behavior in locating HQ food, and (4) how these factors combined to influence nitrogen ingestion throughout the day. Our findings show that behavioral responses to variation in prey quality could allow copepods to rapidly locate small, ephemeral HQ prey patches. Including behavior in current models may help explain patterns of ecological stoichiometry and plankton distributions.

Why is this important? Our results showed that copepods like *Acartia tonsa* can rapidly and effectively use behavior to find HQ prey. This is of great interest because although rarely included in current models, behavioral responses of consumers to small-scale differences in food quality could have large consequences for our understanding of marine ecosystem dynamics and stoichiometry.

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