

The Swimming Behavior of the Calanoid Copepod *Calanus sinicus* Under Different Food Concentrations

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Ming-Ren Chen and Jiang-Shiou Hwang (2018) *Calanus sinicus* is a calanoid copepod and dominant zooplankton species in the coastal waters of the western North Pacific rim. We examined the effects of different food concentrations on the swimming behavior of this species. Adults were video-recorded at 30 frames/s using video equipment that allowed us to follow each freely swimming individual continuously in 1L containers (10 × 10 × 10 cm) with 30 PSU salinity filtered seawater at 20°C. Several behavioral parameters such as swimming trajectories and speed showed distinct changes under different food conditions. The dynamics of swimming states were assessed by the statistical properties of their trajectories. Slow swimming was generally the dominant behavior. Swimming path trajectory decreased at high food concentrations and swimming path entropy decreased when the food concentrations increased.

Key words: Small-scale, Behavior, NDGR, Entropy, Trajectory, Trophic ecology, Feeding strategy.

BACKGROUND

Energy is mainly transferred from lower to higher trophic levels through feeding. Copepods are key species in marine pelagic systems; they are not only a link between primary producers and fish, but also predators of other consumers (Wu et al. 2010). In oceanic ecosystems, planktonic copepods constitute the majority of mesozooplankton biomass (Verity and Smetacek 1996; Hwang and Martens 2011; Sanoamuang and Hwang 2011). By eating and being eaten, this group plays a major role in the flow of matter and energy in pelagic ecosystems (Kiørboe et al. 1998; Hwang and Martens 2011; Sanoamuang and Hwang 2011). Copepod production supports most food webs in the open sea and in this way directly affects pelagic fish populations and the biological pump of carbon into the deep ocean (Ohman

and Hirche 2001). Understanding the regulators of copepod behavior is critical to identifying mechanisms through which copepods handle major challenges - e.g. feeding, survival and reproduction - in their three-dimensional habitat (Kiørboe 2011). Planktonic copepods continuously receive information from their ambient environment and react accordingly through a wide spectrum of behavioural responses (Hwang et al. 2009; Wu et al. 2010).

Observations suggest that copepods exhibit a wide spectrum of behavioural patterns (Hwang et al. 2009; Michalec et al. 2010; Souissi et al. 2010; Wu et al. 2010; Cailleaud et al. 2011; Dur et al. 2011a b; Kiørboe 2011; Lee et al. 2011). Locomotion is a behavioral characteristic that can distinguish genera and even species. Improved video-recording technologies have been very helpful for understanding small scale copepod behavioral

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ecology (Buskey et al. 1987; Yen and Fields 1992; Hwang and Strickler 1994; Strickler and Hwang 1999; Kiørboe et al. 2009; Dahms and Hwang 2010; Chang et al. 2011; Dur et al. 2011b). These technologies allow us to demarcate if behavior is species-specific and reveals important aspects of animal-environment interactions (Fields and Yen 1997; Mazzocchi and Paffenhöfer 1999; Lee et al. 2010; Wu et al. 2011).

The calanoid copepod *Calanus sinicus* is widely spread across shelf waters in the western North Pacific, from Japan to Vietnam. *C. sinicus* is the main food source for several fishes that are important for the fishing industry, such as anchovies and mackerel. In the Bohai Sea, Yellow Sea, and East China Sea, *C. sinicus* is a dominant zooplankton species that accounts for 80% of the zooplankton biomass, indicating it plays an important role in marine pelagic ecosystems (Zhu and Iverson 1990; Chen 1992; Huang et al. 1993; Hulsemann 1994; Li et al. 2003; Hwang and Wong 2005; Chen et al. 2010).

Our objectives were to examine several behavioural responses to different food concentrations through video-recording experiments.

MATERIALS AND METHODS

Animal procurement

Adults *Calanus sinicus* individuals were collected using a plankton sampler with a mesh size of 333- μ m by an oblique haul from surface waters in coastal waters of northeastern Taiwan, next to Kueishan Island, on the 20th January 2008. Once in the laboratory, the copepods were transferred to 1L quartz glass containers filled with filtered (0.22 μ m) seawater of 30 PSU salinity. The copepods were kept at 20°C at a 12:12 L/D cycle over 24 h without additional feeding until experimentation.

Experimental set-up

Three different food concentrations (no-food, low, high) were tested in this study. The response behavior was monitored every 30 minutes at room temperature (20°C). For each of the triplicate experiments, 20 *C. sinicus* females were sorted into glass containers (10 × 10 × 10 cm in dimension, covered by a lid), and acclimated for 1 h before video-documentation began. We used a mixture of the microalgae *Nannochloropsis*

oculata and *Tetraselmis chui* at a ratio of 1:1. The final concentrations of the mixed algae in the experimental containers were 0, 10⁴ and 5 × 10⁴ cells mL⁻¹.

Video equipment and recording

Copepod behavior was documented by video filming. Videos were recorded using dark field illumination in the dark at 20°C. An infrared LED lamp (peak wavelength 910 nm; 1.45 volts) and a DV recorder (Sony HDD) with a modified Schlieren optical system was deployed for filming (see Strickler and Hwang 1999). Repeated observations were made for each experiment in triplicate runs to clarify the variability of swimming behavior among individual copepods and between repeats. The optical system, techniques, and analysis of film sequences were the same as described by Chen et al. (2012).

Characterization of locomotion and trajectories

After the experiments, video sequences were analyzed employing Lab-Track, a manual tracking software program, to digitalize the swimming trajectories of *C. sinicus*. Before using this software, the video was transformed into image sequences using Adobe Premiere software to display images one by one. A trajectory was reconstructed by clicking on the position of the same object in each frame. Only trajectories longer than 45 frames were retained to calculate statistically significant measurements. The data next to the container walls (10 mm away from the wall) were not used for analysis.

Swimming speed calculations

The Pythagorean Theorem ($C^2 = A^2 + B^2$) was applied to obtain distances in pixels and to calculate distance scales for the analysis of video frames. The distance d (mm) between 2 successive video frames was computed from the (x , y) coordinates as follows:

$$d = [(x_{t+1} - x_t)^2 + (y_{t+1} - y_t)^2]^{1/2} \quad (1)$$

Where (x_t , y_t) and (x_{t+1} , y_{t+1}) are copepod positions at times t and $t + 1$ (1/30 sec), respectively. The swimming speed, v , (mm s⁻¹) was then estimated as follows:

$$v = df \quad (2)$$

Here f is the sampling rate of the camera, that is, $f = 30 \text{ frames s}^{-1}$. We calculated average swimming speeds and their standard deviations from individual tracks. Analyses and methodologies generally followed the approaches of Wu and Chen and co-workers (Wu et al. 2010; Chen et al. 2012).

NGDR

The “tortuosity” of trajectories was used to calculate the “Net to Gross Displacement Ratio” (NGDR) (Buskey 1984). $X(n)$ is the 2D position of an individual copepod in the frame n ; $d_i = \|X(i) - X(i-1)\|$ the distance between the position of the individual copepod at frame $i-1$ and frame i , and $\Delta = \|X(n) - X(1)\|$ the distance between the first and last position of the whole trajectory. For a trajectory of n successive frames, the NGDR is defined as follows (see also Wu et al. 2010):

$$NGDR = \frac{1}{\Delta} \sum_{i=2}^n d_i \quad (3)$$

This ratio will be between 0 and 1. Values close to 1 correspond to rectilinear motion, whereas smaller ratios indicate a higher complexity of the swimming path.

Angle

The instantaneous angle - the turning angle defined as the difference in direction between 2 successive moves - is defined as follows:

Angle α is:

$$\alpha = \text{atan2} [\text{imag}(\alpha), \text{real}(\alpha)] \frac{180}{\pi} \quad (4)$$

with

$$\text{imag}(\alpha) = \frac{\|\vec{x} \times \vec{y}\|}{\|\vec{x}\| \|\vec{y}\|} \quad (5)$$

$$\text{real}(\alpha) = \frac{\|\vec{x} \cdot \vec{y}\|}{\|\vec{x}\| \|\vec{y}\|} \quad (6)$$

Diffusion coefficient

Several motile zooplankton can be characterized by a diffusion coefficient (D), in which the way they spread out is similar to molecular diffusion (Jakobsen et al. 2005). We estimated the equivalent diffusion coefficient (mm^2/s) by regression from the root mean square

net length distance covering area (r , mm) as a function of time (t), and varies with time according to:

$$r^2 = 4Dt \text{ for two dimensions (see Berg 1983)} \quad (7)$$

then the resulting diffusion constant is $D = r^2/4t$ (8)

Dynamic analysis

As for velocity, we assigned a swimming state to each frame. Four categories were distinguished with reference to instantaneous velocity as follows:

Fast swimming (FS), in this case, the swimming activity corresponded to a fast jump with speed values above 80 mm s^{-1} .

Slow swimming (SS), this state corresponded to a “cruising” period characterized by an active swimming speed of 1 and 80 mm s^{-1} .

Sink (S) with a downward movement. Swimming speed ranged here between 1 and 8 mm s^{-1} and the direction was slow but directly towards the bottom due to the influence of gravity.

Break (B), with a swimming speed smaller than 1 mm s^{-1} . Here, the copepod was not swimming, but showing minimal activity to avoid sinking.

Various swimming states made it necessary to assess the transition probability between each activity. For example, if the present state was fast swimming, $p(SS|FS)$ provided the probability of entering a slow swimming mode. Dynamic analysis of *C. sinicus* swimming behaviour was performed using averaged values of these transition probabilities.

We used the Shannon entropy analysis of differential swimming states to characterize the complexity in the dynamics. The Shannon entropy was defined as follows:

$$H = -\sum p(A_i) \log p(A_i) \quad (9)$$

Where $p(A_i)$ is the probability mass function of the outcome symbol A_i .

Information theory defines entropy as a measure of the uncertainty associated with a random variable. Accordingly, the higher the entropy, the larger the uncertainty causing a higher behavioural complexity. The average residence time for each state and percentage of the total time spent in each activity were calculated.

RESULTS

In the dark (infrared light) environment, *Calanus sinicus* displayed different swimming behaviours at different food concentrations (Figs. 1a-c). In the absence of food, *C. sinicus* showed the least complex swimming behaviour. When food was offered, *C. sinicus* swimming trajectories became more complex patterns, spiral swimming occurred, and the radius of the spiral increased with increasing food concentrations.

Swimming speed, NGDR and turning angle

In this study, 284 swimming trails were recorded. The swimming speed, NGDR and angle of change for *C. sinicus* at different food concentrations were analyzed (Table 1). In the absence of food (N), the swimming speed of *C. sinicus* ranged between 4.14 mm/s and 24.71 mm/s, with an average speed of 8.86 ± 3.63 mm/s and NGDRs ranging from 0.01 to 0.89, with an average of 0.28 ± 0.21 . At low algal concentrations, the swimming speed of *C. sinicus* ranged from 3.25 mm/s to 19.43 mm/s, with an average speed

of 7.01 ± 2.35 mm/s and NGDRs ranging from 0.01 to 0.96, with an average of 0.28 ± 0.22 . The median value of NGDR measured at different food conditions was highest at high environmental food concentrations and lowest at low food concentrations. There was a significant difference in NGDR values between the absence of food and the provision of high concentrations of food, as shown by the Mann-Whitney test (Fig. 2).

At high concentrations of algae (H), the swimming speed of *C. sinicus* was between 2.85 mm/s and 24.65 mm/s, with an average velocity of 8.68 ± 3.84 mm/s and NGDRs ranged from 0.01 to 0.83, with an average of 0.36 ± 0.23 . The results showed that *C. sinicus* had the lowest average swimming speed and lowest median speed at low food concentrations (L) (Fig. 3).

As for the turning angles of *C. sinicus*' swimming trajectory in the three food concentrations, the median value was the lowest at high food concentrations (49.38°) and highest when food was absent (70.68°). At low food concentrations the median angle was 63.20° (Fig. 4).

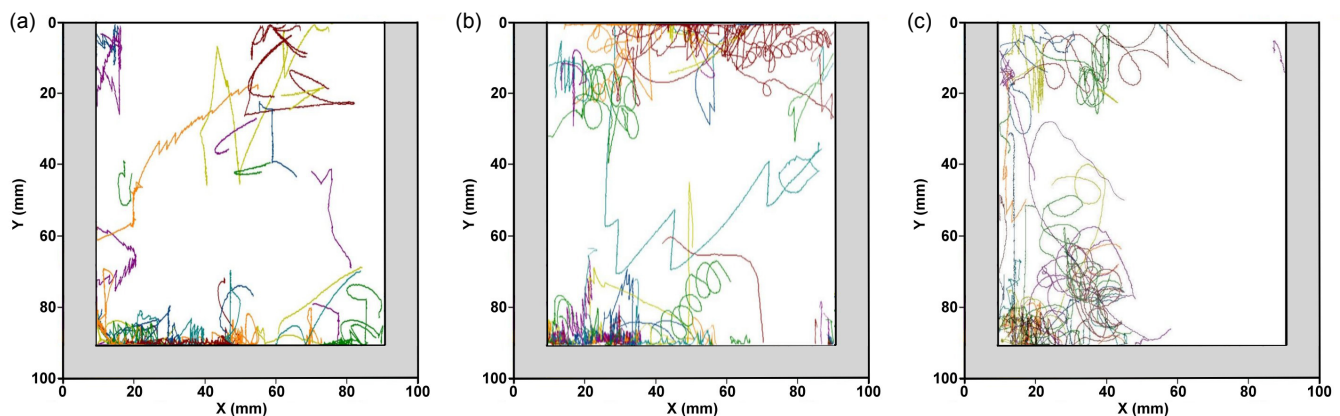


Fig. 1. *Calanus sinicus* swimming trajectories under experimental treatments: (a) no food, (b) low food concentrations and (c) high food concentrations.

Table 1. Experimental conditions and data, including the number of tracks and data for statistical analysis

	No. of tracks	No. of data points
<i>T in situ</i> (°C)	20	
No. of individuals	20	
No Food	95	21731
Low Food	115	39357
High Food	74	18950

Diffusion coefficient

The median value of the diffusion coefficient (D) was 80.80 mm²/s at high concentrations of food, 64.28 mm²/s at low food concentrations, and 78.80 mm²/s when food was absent.

Dynamic analysis

The analysis of the Shannon entropy (H)

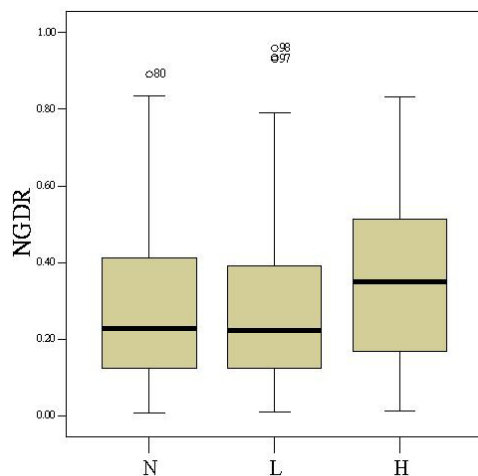


Fig. 2. Box plot showing the median (central mark), the 25th and 75th percentiles (edges of the box), the lowest and highest data points (whiskers), and outlier data values of Net to Gross Displacement Ratios (NGDR). NGDR were calculated from trajectories displayed by *Calanus sinicus* females at no food (N), low food (L) and (H) high food conditions.

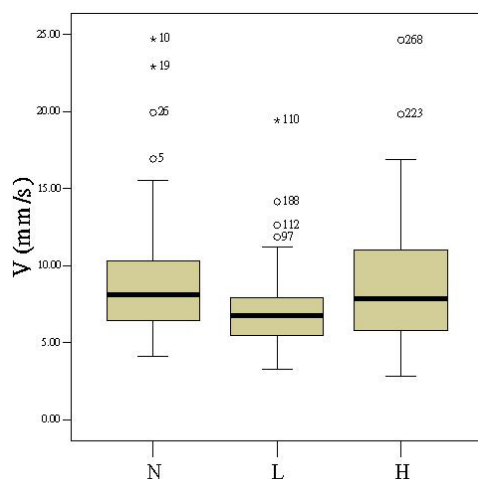


Fig. 3. Box plot showing the median (central mark), the 25th and 75th percentiles (edges of the box), the lowest and highest data points (whiskers), and outlier data values of the average instantaneous swimming velocity (V), calculated from trajectories displayed by *Calanus sinicus* females in no food (N), low food (L) and (H) high food conditions.

results showed that entropy was higher than 0.5 at all food concentrations. This indicates that there is a lot of uncertainty in how *C. sinicus* behave. At no food, the value was 0.71 ± 0.07 . At low concentration of food the entropy was 0.64 ± 0.10 , at high concentrations of food the entropy was 0.63 ± 0.14 . In the presence of food, the entropy was relatively low, indicating that the state of uncertainty in swimming behavior was low and dynamic behavioral changes were relatively small.

We analyzed the proportion of other behavioral activities in *C. sinicus* (such as fast and slow swimming, sinking, breaks) and the results are summarized in figure 5. These results showed that *C. sinicus* swimming activity increased at high concentrations of food, meaning they took shorter breaks, accounting for 28.23% of all activity times, and sinks account for 6.80% of all activity times lower than other food concentrations, and the proportion of slow swimming increases, accounting for 64.41%, higher than at other food concentrations. In the absence of food, *C. sinicus* remained in a state of sinking (14.04%), and fast swimming (0.95%) was observed. At low food concentrations, the swimming activity of *C. sinicus* decreased and the animals spent more time in the resting state (34.02%).

In general, the trend of *C. sinicus* swimming activity change will be different in different food conditions. Food supply enhances its swimming activities; however, when the food concentration increases, the probability of entering the slow

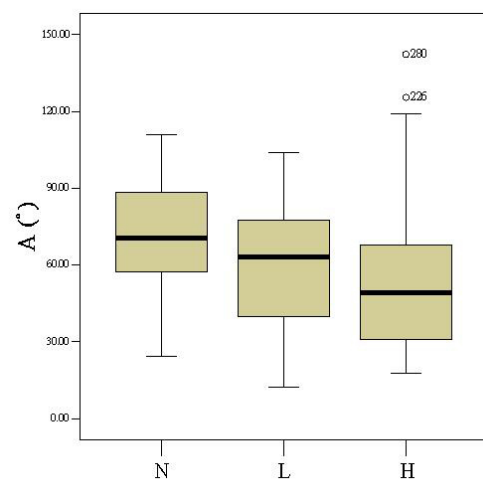


Fig. 4. Box plot showing the median (central mark), the 25th and 75th percentiles (edges of the box), the lowest and highest data points (whiskers), and outlier data values of the average instantaneous angle (A), calculated from trajectories displayed by *Calanus sinicus* females at no food (N), low food (L) and (H) high food conditions.

swimming state increases significantly.

The probability of *C. sinicus* changing from the resting state to slow swimming was highest at high food concentrations, $P(B|SS) = 81.87\%$, in the absence of food this was lowest ($B|SS$) = 66.65%. The probability that *C. sinicus* changes from a resting state to slow swimming at low food concentrations was 72.83%.

DISCUSSION

Slow swimming accounts for the highest proportion of *Calanus sinicus* swimming behavior, more than 50% (Fig. 6). At the same time, *C. sinicus* swimming activities increased as food concentrations increase (Fig. 5). At high food concentrations, the Shannon entropy was low.

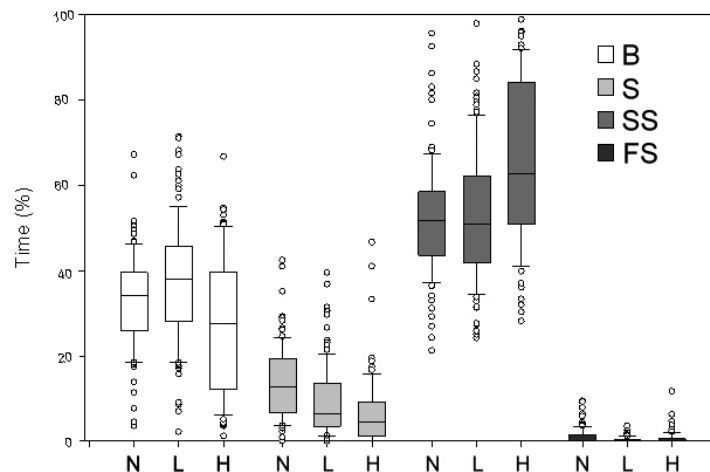


Fig. 5. Box plot showing the median (central mark), the 25th and 75th percentiles (edges of the box), the lowest and highest data points (whiskers), and outlier data values of means of total activity (%) for each 4 states break (B), sink (S), slow swimming (SS), and fast swimming (FS) at no food (N), low food (L) and (H) high food conditions.

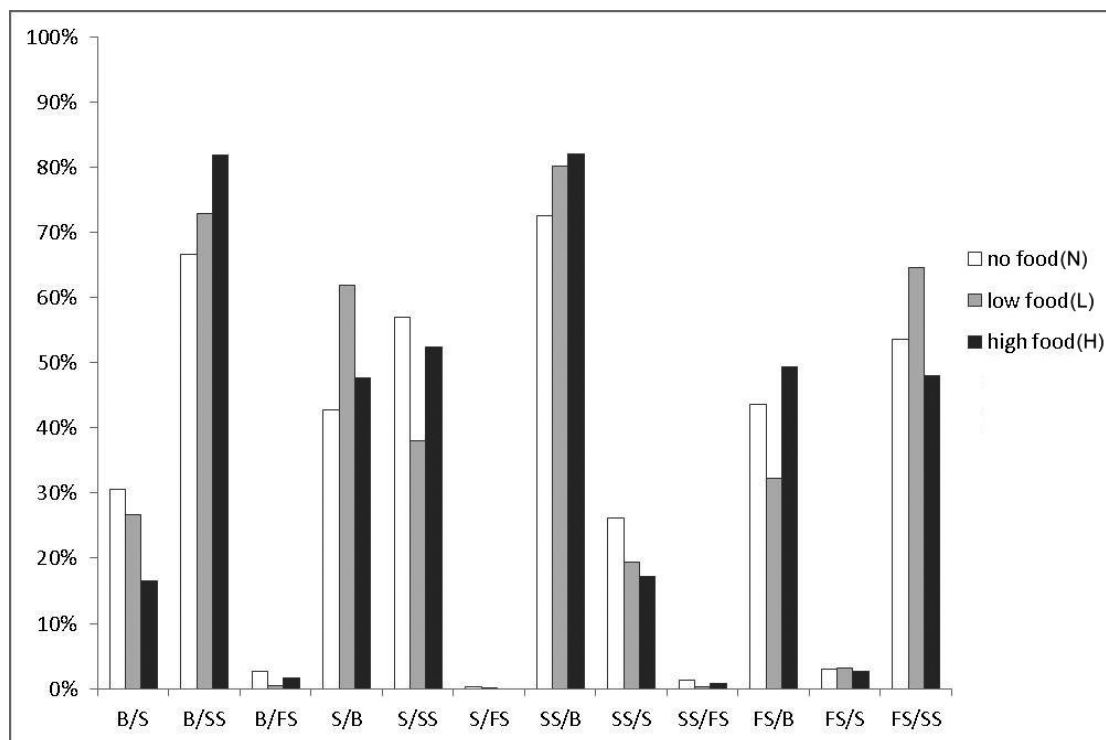


Fig. 6. Average of transition probabilities (P) between each swimming state, i.e. fast swimming to slow swimming (FS/S), fast swimming to break (FS/B) sink to slow swimming (S/SS) at no food (N), low food (L) and high food (H) conditions.

That means that the pattern of swimming behavior was relatively predictable, and the combination of the same swimming state was repeated more frequently.

The swimming behavior trajectories of *C. sinicus* were quite different in the presence or absence of food (see Figs. 1a-c). In the absence of food or at low food concentrations, *C. sinicus* covered a wide area by foraging, probably because it was searching a larger area for food.

In order to increase the chances of capturing food, animals usually change their behavioral patterns, or change the speed of locomotion (Pyke et al 1977). Mazzocchi and Paffenhöfer (1999) found that adult *Clausocalanus furcatus* females circle around when feeding. The spiral swimming behavior can cause the copepods to search for more food in a small range of water, thereby improving their feeding efficiency (Gerritsen and Strickler 1977). In this study, *Calanus sinicus* also showed helicoidal swimming behavior (Fig. 1b, Fig. 1c) as long as there was food in the environment, demonstrating that this spiral swimming behavior is closely related to feeding (see also Buskey 1984; Cowles and Strickler 1983). Copepods change their swimming behavior patterns because of differences in food conditions (Wong and Sprules 1986). Wong (1988) found that *Metridia pacifica* would present non-randomized swim-feeding that reduces the chances of being preyed on while feeding. Williamson (1981) found that when *Mesocyclops edax* was ingesting, it would increase its rotational speed in areas where food concentrations were relatively high. The results of our study also showed the changes in swimming activity and behavioral trajectories of *C. sinicus* at different food concentrations. The speed of spiral swimming at high food concentrations (11.37 ± 2.39 mm/s) was faster than at low food concentrations (8.77 ± 1.69 mm/s). At higher activity, larger amounts of water can be screened and provide more efficient feeding (Kiørboe 2011). Yen et al. (2011) have argued that sinking (terminal velocity) is faster than swimming. In a future study we will also reconcile such difference in our definitions and show sensitivity analysis results. This should explain how the cutoff value for speed affects the outcome of an analysis. However, *C. sinicus* may also increase their swimming speed to leave the food patch. At high food concentrations, there is no need for extended foraging activity and energy for this can be saved or allocated to other activities, such as reproduction. Optimality varies between feeding types.

Different copepods may have different swimming behaviors such as gliding, jumping, and sinking (Wong and Sprules 1986). Copepods may adjust their behavior patterns due to different food conditions. Some copepod species may have a rest in the absence of food, keep more energy to feed or move to a richer area of food (Frost 1975; Reeve and Walter 1977; Cowles and Strickler 1983; Buskey 1984; Wong 1988; Chen et al. 2012). This indicates that planktonic food may change the swimming behavior of some marine copepods. This study discovered that *C. sinicus* may rest and sink low food concentrations rather than showing more active behavior at high environmental food concentrations.

The choice of diffusion coefficient as a proxy to copepod behavior is likely an oversimplification. Seuront and Stanley (2014) have demonstrated that, when presented with chemical cues, copepod behaviors diverge from Levy and Brownian motion.

CONCLUSION

This study provided only a preliminary understanding of the effects of different food conditions on the swimming behavior of adult female *Calanus sinicus*, there may be different behavioral responses at different ontogenetic stages and sex, as well as upon environmental changes (Titelman and Kiørboe 2003; van Duren and Videler 1995). Our results revealed the effects of food on the swimming behaviors of adult female *C. sinicus*. However, swimming ability changes throughout ontogeny and behavioral responses change with different environments (van Duren and Videler 1995; Titelman and Kiørboe 2003). Therefore, similar studies should be extended to males and other developmental stages, including nauplii and copepodites. This would provide a more comprehensive understanding of *C. sinicus* behavioral strategies and its effects on life history trade-offs in different trophic environments. Based on our results, we will study different ontogenetic changes and sex of *C. sinicus* feeding behavior, which will improve our understanding of feeding strategies within the life history of *C. sinicus*.

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Competing interests: MRC and JSH declare that they have no conflict of interest.

Availability of data and materials: The data and materials that support the findings of this study are available from the corresponding author upon reasonable request.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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