Copepod feeding strategy determines response to seawater viscosity: videography study of two calanoid copepod species

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Keywords: copepods, zooplankton, seawater viscosity, feeding mechanism, micro-particle tracking velocimetry (μPTV)

Summary statement

Using high-speed microvideography to resolve individual-level movements of copepods, we find that calanoid copepods, depending on feeding strategy, respond differently to changes in seawater viscosity but similarly to diet.

Abstract

Calanoid copepods, depending on feeding strategy, have different behavioral and biological controls on their movements, thereby responding differently to environmental conditions such as changes in seawater viscosity. To understand how copepod responses to environmental conditions are mediated through physical, physiological, and/or behavioral pathways, we used high-speed microvideography to compare two copepod species, *Acartia hudsonica* and *Parvocalanus crassirostris*, under different temperature, viscosity, and dietary conditions. *Acartia hudsonica* exhibited "sink and wait" feeding behavior and typically responded to changes in seawater viscosity; increased seawater viscosity reduced particle-capture behavior and decreased the size of the feeding current. In contrast, *P. crassirostris* continuously swam and did not show any behavioral or physical responses to changes in viscosity. Both species showed a physiological response to temperature, with reduced appendage beating frequency at cold temperatures, but this did not generally translate into effects on swimming speed, feeding flux, or active time. Both copepod species swam slower when feeding on diatom rather than dinoflagellate prey, showing that prey type mediates copepod behavior. These results differentiate species-specific behaviors and responses to environmental conditions, which may lead to better understanding of niche separation and latitudinal patterns in copepod feeding and movement strategies.

Introduction

As an important link in the marine food web (Cushing, 1989; Levinson et al., 2000; Turner, 2004) with influence over biogeochemical cycles (Jónasdóttir et al., 2015), copepod movements may have broad impacts on marine ecosystems. In the nutritionally dilute ocean, planktonic copepods must search approximately 10^6 body volumes of seawater each day to consume adequate food (Kiørboe, 2011; Kiørboe and Jiang, 2013). From a fluid dynamical point of view, a copepod's feeding current depends on its excess weight (Jiang et al., 2002a; Jiang et

al., 2002b; Kiørboe and Jiang, 2013; Strickler, 1982). However, there are also biological and physiological constraints on the feeding current, leading to a diversity of movement and feeding strategies (Kiørboe, 2010; Kiørboe, 2011). Copepods must beat their cephalic appendages to drive the feeding current, and appendage movement may be constrained by metabolism, temperature, and seawater viscosity. Ingestion also depends on active feeding time, which is under behavioral control and may be altered according to environmental conditions. Additionally, copepods with different feeding strategies may have different behavioral responses. For example, copepods that can use multiple feeding strategies (Kiorboe *et al.*, 1996) can switch to the most advantageous method, while copepods that use only one mechanism cannot show this response. These biological constraints on feeding have seldom been studied.

At 0 ºC, the viscosity of 36 ‰ salinity seawater is 1.89×10^{-3} kg m^{-1} s^{-1}, whereas at 30 ºC, its viscosity is only 0.86×10^{-3} kg m^{-1} s^{-1} (Miyake and Koizumi, 1948). Biogenic compounds, such as the mucus released by some bloom-forming algae, may also increase seawater viscosity (Seuront et al., 2006). Due to their small size (~0.5 - 10 cm), copepods are characterized by low Reynolds numbers of 10^{-2} to 10^{3} (Yen 2000) ($Re = \rho\, u\, L\, /\, \mu$, where ρ is seawater density, μ is seawater dynamic viscosity, u is the speed of the organism, and L is the length of the organism). In this low-to-intermediate Re regime, movements are impacted by seawater viscosity.

Therefore, several temperature-related responses in the zooplankton can be attributed to a physical response to seawater viscosity. Seawater viscosity is responsible for reduced ingestion at cold temperature (Bolton and Havenhand, 1998; Podolsky, 1994; Tyrell and Fisher, 2019) and reduced swimming speed at cold temperature (Larsen et al., 2008). Yet, we are unaware of any laboratory studies that used videography to directly investigate the physical and behavioral pathways through which seawater viscosity and temperature impact copepods.

We used high-speed microvideography to study the swimming and movement behavior of two species of common temperate copepods, *Acartia hudsonica* and *Parvocalanus crassirostris*, which are both found along the eastern coastal United States (Milligan et al., 2011; Turner, 1981). *Acartia* spp. have a cephalothorax length of ~0.8 - 1.0 mm and utilize a "sink and wait" feeding strategy, with short feeding periods (< 0.5 s) interspersed with longer periods of sinking (> 1 s) (Kiørboe et al., 1996). In contrast, *P. crassirostris* have a cephalothorax length of ~0.3 - 0.4 mm and spend more time creating a feeding current (pers. obs.; Bradley et al., 2013). The contrast between these two species may illuminate the advantages and trade-offs of each

feeding strategy. Because diet influences copepod response to seawater viscosity (Tyrell and Fisher, 2019), we fed the copepods two unialgal diets: *Thalassiosira weissflogii*, a non-motile diatom, and *Prorocentrum mimimum*, a motile dinoflagellate. The natural ranges of both phytoplankton species overlap with the ranges of the two copepod species (Turner, 1981; Hargraves, 2002; Heil et al., 2005; Sorhannus *et al.*, 2010; Milligan et al., 2011). Species-level resolution of copepod ingestion patterns in the field is scarce, but both *P. crassirostris* (Calbet *et al.*, 2000) and the *A. hudsonica* congener *A. tonsa* (Bollens and Penry, 2003) consume small autotrophic cells, including diatoms and flagellates; therefore, *T. weissflogii* and *P. minimum* are representative dietary species. In all experiments, we separated the effect of viscosity from the effect of temperature by manipulating seawater viscosity with the non-toxic polymer polyvinylpyrrolidone (PVP) (Podolsky and Emlet, 1993; Riisgård and Larsen, 2007; Tyrell and Fisher, 2019) in addition to altering the temperature.

We hypothesized that temperature responses would be partly or fully explained as a viscous response. We hypothesized that copepod movements would be slowed and activity would be decreased by increased seawater viscosity. Because our previous research has shown that copepod response to viscosity differs depending on diet (Tyrell and Fisher, 2019), we hypothesized that copepod behavior and movement would be also affected by diet. Because *A. hudsonica* is found at cooler temperatures and is a less active swimmer than *P. crassirostris*, we hypothesized that *A. hudsonica* would be less sensitive to changes in viscosity.

Materials & Methods

Phytoplankton cultures

Prorocentrum minimum (clone CCMP 696) and *Thalassiosira weissflogii* (clone CCMP 1336) cultures were used. Cultures were maintained in sterile filtered (0.2 μm) seawater from Woods Hole, MA (salinity of 32 - 35 ‰) supplemented with f/2 nutrients (Guillard and Ryther, 1962). Cells were kept on a 14:10 light:dark cycle at ambient temperature (18 - 21 ºC).

Copepod cultures

Acartia hudsonica (Pinhey, 1926) were collected from Woods Hole, MA, USA one to two days before videography trials. AlgaGen ReefPods™ cultures of *Parvocalanus crassirostris* (Dahl F., 1894) were ordered from LiveAquaria (Rhinelander, WI, USA) in May 2018. Copepods were maintained in the laboratory before experiments and fed ad libidum with a mixture of *P. minimum*, *T. weissflogii*, and *Isochrysis galbana*. All copepods were kept on a 14:10 light:dark cycle at ambient temperature (18 - 21 ^{o}C) until shortly before trials.

Experimental treatments

The three experimental treatments used 0.2 μm filtered water (salinity of 32 - 35 ‰) collected from Woods Hole, MA, USA. Treatments were: (1) 10 ^{o}C seawater, (2) 20 ^{o}C seawater, and (3) 20 ^{o}C seawater with 0.12% w/v polyvinylpyrrolidone (PVP, Sigma-Aldrich, SID 24899318) added to create a viscosity similar to that in 10 ^{o}C seawater (Table S1). The PVP polymer is non-toxic and addition of 0.12% w/v enabled manipulation of seawater viscosity without affecting temperature or seawater density (Podolsky and Emlet, 1993; Riisgård and Larsen, 2007; Tyrell and Fisher, 2019).

Seawater samples were taken from each experiment and stored at 4 ^{o}C in the dark until analysis. The kinematic viscosity of the experimental water was measured at the appropriate temperature using an Ubbelohde viscometer (Sigma-Aldrich UBBEL02UKC) and the equation supplied by the manufacturer. Kinematic viscosity was converted to dynamic viscosity using the equation: dynamic viscosity = density × kinematic viscosity.

Videography system

A high-speed microscale imaging system (HSMIS) was used to record high-resolution 2D digital videos at 2000 frames s^{-1}. The HSMIS consists of a Photron (San Diego, CA, USA) FASTCAM SA3 120K monochrome video camera that takes 1024×1024-pixel resolution images at frame rates up to 2000 frames s^{-1}. The camera is mounted horizontally with a 150 mm focal length objective lens plus an infinity-corrected, long-working-distance microscope objective (4×/0.10 18.5 mm working distance) to yield a field-of-view of a vertically oriented area of ~4.8×4.8 mm, or approximately 6 *A. hudsonica* body lengths or 12 *P. crassirostris* body lengths. A 1-Watt white LED light source was collimated to provide backlit illumination in which light

was shined toward the camera through a prepared flask placed in front of the microscope objective. The field-of-view was focused at the center of the flask, which was at least 1 cm (~12 or 25 copepod body lengths) away from flask walls. The HSMIS of different optical specifications has been previously used for quantitative microvideography and micro particle image velocimetry (Jiang and Johnson, 2017; Jiang et al., 2018; Du Clos and Jiang, 2018; Jiang & Paffenhöffer, 2020). The HSMIS has the advantage of achieving sharp imaging under low illumination. Summaries of video conditions can be found in Table S1.

Experimental measurements and analysis

One day prior to recording videos, 28-66 adult female copepods (Table S1) were placed into 20 mL (*P. crassirostris*) or 40 mL (*A. hudsonica*) treatment seawater. Within each experimental treatment, there were three dietary/particle conditions: (1) *P. minimum* cells only, (2) *T. weissflogii* cells only, and (3) *T. weissflogii* cells with polystyrene tracking particles added (3 µm diameter) to help trace the seawater movement around the copepods (hereafter, these three treatments are referred to as the diet treatments). Copepods sometimes consumed a small portion of the cells and tracking particles during the 2 - 8 hours of videography. The copepods were acclimated for > 13 hours in seawater of the appropriate temperature and viscosity with algal cells added (Table S1). The copepods were kept in indirect light on a 14:10 light:dark cycle during this acclimation.

A total of 519 videos were recorded according to the following procedure: a live video feed was monitored. When a copepod swam across the field of view, the previous 2.7s of footage was captured by manually triggering the camera. The footage was then edited to include only the period of time during which the copepod was in the frame, and it was saved. The saving process took ~5-10 minutes, after which the procedure was repeated. A target of 25-30 videos of each copepod species were saved for each of the nine diet-treatment combinations. Sample sizes of video data are constrained by the intensive data collection process, and it is not always possible to know if a video will be suitable for all analyses at the moment it is collected. Through bootstrap analysis of 1,000 sets of random data, we calculated that ≥5 suitable videos per diet-treatment combination would yield a power of ≥0.9 for an effect size of a 50% reduction in the mean if the standard deviation was ≤50% of the mean, while ≥15 suitable videos per diet-treatment combination would yield a power of ≥0.8 for an effect size of a 25% reduction in the

mean if the standard deviation was ≤50% of the mean. Therefore, our experimental design was suitable to detect effects.

Most videos contained only one copepod, although a small portion of videos contained multiple copepods. Because the field of view was larger in terms of *P. crassirostris* body lengths over *A. hudsonica* body lengths, the larger-scale movements of *P. crassirostris* may have been better captured, while the individual-level details of *A. hudsonica* may have been better captured. The maximum video length was 2.7s, and the average video time for both copepod species was 2.5s ± 0.5s SD. In all analyses, only adult females were considered.

Flow fields, copepod movements, appendage beating frequency, proportion of time spent swimming, and swimming speed were analyzed. Analyses were done in R (version 3.6.1) or Python (version 2.7.17); specific software package details are shown in Table S2. Depending on the analysis, videos were included if the copepod was in focus, swimming in the plane of the camera, and/or if its movements could be resolved by eye; analyses are described below.

Particle tracking: feeding flux

In the videos with tracking particles added, ≥ 100 frames (*A. hudsonica*) or ≥ 1000 frames (*P. crassirostris*) from videos with consistent, in-focus copepod feeding movements were analyzed using a micro-particle tracking velocimetry (μPTV) method in Python using the libraries *trackpy* and *OpenCV2*. All particles in an 800×800-pixel (~3.8×3.8 mm) window (*A. hudsonica*) or 400×400-pixel (~1.9×1.9 mm) window (*P. crassirostris*) around the copepod were tracked, and the particle trajectories were recorded. The trajectories were then centered to the copepod's frame of reference. The speed of each particle was calculated from its net displacement divided by the duration of time that it was in the video.

For each video, the speed of the feeding current was calculated as the mean speed of all particles that crossed a line positioned one body length forward from the copepod's center of mass. Depending on the orientation of the copepod, the line's width was equal to the width of the antennae (dorsoventral orientation) or two body widths (sagittal orientation). This feeding current speed was then used to calculate the feeding flux (the amount of seawater moving past the copepod's mouthparts per unit time) by assuming an elliptical shape of the cross section of the feeding current, with the long axis equal to the width of the antennae and the short axis equal

to two body widths. The effect of temperature/viscosity treatment on feeding flux was determined with one-way ANOVA with Tukey's post-hoc test.

Copepod movements

Copepod movements were classified as sinking, swimming, twitching of the first antennae or urosome, hopping, or jumping. The copepod was classified as sinking when it was motionless. Swimming was defined as rhythmic beating of the feeding appendages (cephalic appendages). During swimming, the copepods sometimes twitched the urosome or first antennae, and this was noted as well. Large hops were defined as up to two (*A. hudsonica*) or three (*P. crassirostris*) rapid beats of the swimming appendages. *Acartia hudsonica* displayed more nuanced hopping behavior, so *A. hudsonica* small hops were categorized separately and defined as incomplete deployment of the swimming appendages in conjunction with movement of the first antennae and/or urosome that displaced the copepod a short distance. Jumping was defined as more than two (*A. hudsonica*) or three (*P. crassirostris*) beats of the swimming appendages. All movements where the copepod was relatively in-focus, but not necessarily moving in the plane of focus, were assessed. 287 *A. hudsonica* copepods were analyzed, with copepods in the video for an average of 2.3s ± 0.7s SD (minimum length 0.1s). 235 *P. crassirostris* copepods were analyzed, with copepods in the video for an average of 2.4s ± 0.7s SD (minimum length 0.05s).

The number of twitches, hops, and jumps were analyzed by Generalized Linear Models (GLMs), with temperature/viscosity treatment, diet, and length of video as covariates. The negative binomial distribution provided a better fit of the data over the Poisson distribution as determined by comparison of Akaike's Information Criterion with small sample size correction (AICc) and so was used for all analyses, except in the case of *P. crassirostris* jumps, which was fit with a Poisson model because the negative binomial model did not converge. For each movement, the statistical importance of treatment, diet, and the interaction between treatment and diet were determined by χ^2 Likelihood Ratio Tests comparing full and reduced models (comparisons detailed in Table 1). Groupwise differences for each statistically significant factor were determined by creating single-factor zero-intercept GLMs and comparing coefficient estimates; if the 95% confidence interval of coefficient A did not contain the estimate of coefficient B, and vice versa, coefficients A and B were considered statistically different.

Appendage beating frequency

Appendage beating frequency was counted manually for all swimming copepods with visible and identifiable feeding appendages (210 *A. hudsonica* copepods and 169 *P. crassirostris* copepods). The method of counting was tailored to the specific movement patterns of each copepod species.

For *P. crassirostris*, the second antenna and the maxilliped beat in time, and the frequency of this beating was counted by recording the frame numbers at the start of five consecutive beating cycles; average appendage beating frequency for one cycle was then calculated. The start of the appendage beating cycle was arbitrarily defined as the frame when the second antenna and/or the maxilliped (whichever was most visible) returned to a recognizable, cyclic position. Beating frequency was counted in this way three times per video, at manually-selected periods approximately evenly distributed throughout the full amount of time during which the copepod was swimming. Appendage beating frequencies were only recorded during periods when the copepod was not twitching the urosome, appendages, or first antennae; these behaviors may indicate particle capture or rejection and may result in non-uniform beating of the feeding appendages. Because the interaction between temperature/viscosity treatment and diet was statistically significant, the effect of the three diets and three temperature/ viscosity treatments on *P. crassoristros* appendage beating frequency was analyzed by two-way ANOVA with Type III error.

For *A. hudsonica*, the appendage beating frequency was measured by recording the beating of the maxilliped. Since *A. hudsonica* beat its appendages less rhythmically and for a shorter average duration compared to *P. crassirostris*, the beginning frame of all beat cycles was recorded and defined as the frame when the maxilliped first moved away from the body. Then, the first frame when the maxilliped returned to the body and the last frame when the maxilliped returned to the body were both recorded. Appendage beating frequency was calculated as the time between the first return of the maxilliped and the final return of the maxilliped, divided by the number of beats in between (one fewer than the total number of beats). The average appendage beating frequency for each *A. hudsonica* in each video with a visible maxilliped was determined. Because the interaction between temperature/viscosity treatment and diet was not

statistically significant, the effect of the three diets and three temperature/viscosity treatments on appendage beating frequency was analyzed by two-way ANOVA with Type II error.

Proportion of time spent swimming

The total number and duration of swimming periods were determined for each copepod in each video. "Swimming periods" were classified as times when the copepods were rhythmically beating their feeding appendages, and did not include hops or jumps. The proportion of each video spent swimming was calculated by dividing the swimming time by the total time that the copepod was in the video. Videos with no swimming were included as zeroes in the analysis.

For *P. crassirostris*, the first and last frames with movement of the feeding appendages were recorded for each swimming period. 20 out of 235 *P. crassirostris* copepods did not swim. For *A. hudsonica*, swimming was recorded in conjunction with appendage beating frequency measurements (see above). The total time spent swimming was calculated as the difference in time between the first movement of the maxilliped and the final return of the maxilliped, summed over all feeding periods in the video. 72 out of 285 *A. hudsonica* copepods did not swim. The proportion of time spent swimming was compared across the three diets and three temperature/viscosity treatments with the length of the video included using ANCOVA using Type II error if the interaction between temperature/viscosity treatment and diet was not statistically significant and Type III error if the interaction was statistically significant. Tukey's post-hoc test was performed following ANCOVA.

Swimming speed

The coordinates of copepods swimming in the plane of focus were obtained using ImageJ (versions 1.52a and 1.52q) and corrected for background movement by subtracting the movement of a randomly-selected background particle. The coordinates were then smoothed using a fourth-order Savitsky-Golay filter with a 23-point window (Jiang and Kiørboe, 2011) and speed was calculated by taking the first derivative of the copepod's position. The average swimming speed was calculated for feeding periods, defined as periods when the copepod was rhythmically beating its feeding appendages. Only periods longer than 100 frames (0.05 s) (*A. hudaonica*) or 450 frames (0.2 s) (*P. crassirostris*) with no twitching were considered. Speeds

were broken into three categories: (1) copepod oriented upwards with net movement upwards (average video lengths of 0.8s ± 0.6s SD (99 *P. crassirostris* feeding periods) and 0.1s ± 0.07s SD (98 *A. hudsonica* feeding periods)); (2) copepod oriented upwards but with net movement downwards (average video lengths of 1.0s ± 0.7s SD (79 *P. crassirostris* feeding periods) and 0.1s ± 0.06s SD (94 *A. hudsonica* feeding periods)); and (3) copepod oriented downwards with net movement downwards (average video lengths of 0.7s ± 0.5s SD (24 *P. crassirostris* feeding periods) and 0.1s ± 0.07s SD (31 *A. hudsonica* feeding periods)). The copepods were never oriented downwards with net movement upwards.

Within each video, each copepod's swimming speed was averaged across all swimming periods with the same orientation and displacement directions. Because no interactions between temperature/viscosity treatment and diet were statistically significant, two-way ANOVA with Type II error was used to compare the effects of the three diet and three temperature/viscosity treatments on copepod speeds for each orientation/displacement combination.

Interpretation of results

In all of our analyses, we interpreted the effects of seawater viscosity and temperature according to the following patterns. If there was no difference between the 20°C treatment and the high viscosity treatment, it was determined that viscosity did not have an effect. If there was no difference between the 10°C treatment and the high viscosity treatment, it was determined that temperature did not have an effect.

Results

Particle tracking: feeding flux

Fig. 1 shows examples of the flow fields around *A. hudsonica* and *P. crassirostris*. The feeding flux of *A. hudsonica* was statistically decreased by viscosity, but unaffected by temperature (Tukey's post-hoc, $p < 0.05$, following one-way ANOVA, $F_{2,3} = 24.2$, $p = 0.014$) (Table 2). After multiplying by the proportion of time spent swimming, *A. hudsonica* cleared 0.1 - 0.2×10^6 body volumes (4.7 - 8.7 mL) of seawater per day at high viscosity (regardless of temperature); at 20 °C with unchanged viscosity, *A. hudsonica* cleared 0.9×10^6 body volumes (32.5 mL) per day (Table 2). The feeding flux of *P. crassirostris* was not affected by seawater

viscosity or temperature (ANOVA, $F_{2,10} = 0.40$, $p = 0.68$) (Table 2). *Parvocalanus crassirostris* cleared 1.4 - 1.6×10^6 body volumes (6.4 – 9.4 mL) per day after multiplying by the proportion of time spent swimming (Table 2).

Movements

Examples of copepod movements can be viewed in the Supplemental Materials (Supplemental Movies 1-3). These videos replay at 20 Hz (100x slower than real time).

Acartia hudsonica movements primarily included hops, sinking, and short swimming periods (average length of 0.089s ± 0.068s SD, n = 871 feeding periods) (Table 3). *Acartia hudsonica* displayed fewer twitches at high viscosity, regardless of temperature (median number of twitches per video reduced from 2 to 1) (Tables 1, 3). *Acartia hudsonica* small hops, large hops, and jumps were not affected by temperature/viscosity treatment (Tables 1, 3). Diet did not affect any *A. hudsonica* movements (Tables 1, 3).

Parvocalanus crassirostris behavior primarily included long swimming periods (average length of 1.55s ± 0.96s SD, n = 293 swimming periods; this is an underestimate because many swimming periods continue beyond the duration of the video) with twitches of the first antennae and/or urosome (Table 3). There was no effect of temperature/viscosity treatment or diet on *P. crassirostris* twitching, hopping, or jumping (Tables 1, 3).

During the swimming periods, copepods of both species rhythmically moved their feeding appendages and typically were displaced through the water (i.e., no "hovering").

10 randomly selected videos of each copepod species were re-checked for consistency, which showed that movements were reliably scored. There was small variation in classification of hops and twitches of *A. hudsonica* (3/31 classified differently). 8/10 *P. crassirostris* videos counted the same number of twitches when re-checked and 2/10 videos varied. Hop counts for *P. crassirostris* and jump counts for *A. hudsonica* and *P. crassirostris* were all 100% repeatable.

Appendage beating frequency

A. hudsonica appendage beating frequency (Fig. 2) was affected by temperature/viscosity treatment (two-way ANOVA, $F_{2,201} = 57.41$, $p < 1\times10^{-7}$). Diet also had an effect (two-way ANOVA, $F_{2,201} = 4.62$, $p = 0.011$), and there was no interaction between diet and temperature/viscosity (two-way ANOVA, $F_{4,201} = 0.87$, $p = 0.48$). Appendage beating was

significantly faster at 20 ºC than at 10 ºC regardless of viscosity (Tukey's post-hoc following two-way ANOVA, $p > 0.05$), and appendage beating was significantly faster when feeding on *T. weissflogii* with tracking particles compared to *T. weissflogii* without tracking particles (Tukey's HSD following two-way ANOVA, $p > 0.05$).

P. crassirostris appendage beating frequency (Fig. 2) was affected by temperature/viscosity treatment (two-way ANOVA, $F_{2,160} = 160.29$, $p < 1\times10^{-7}$), but diet had no effect (two-way ANOVA, $F_{2,160} = 1.78$, $p = 0.17$). The interaction between diet and temperature/viscosity was statistically significant (two-way ANOVA, $F_{4,160} = 3.32$, $p = 0.012$). Appendage beating was significantly faster at 20 ºC than at 10 ºC, regardless of viscosity (Tukey's post-hoc following two-way ANOVA, $p > 0.05$).

A random selection of 12 *A. hudsonica* videos and 10 *P. crassirostris* videos were re-checked, which showed that appendage beating frequency measurements were consistent and repeatable (paired t-test, *A. hudsonica*: $t_{11} = 0.14$, $p = 0.89$; *P. crassirostris*: $t_9 = 0.26$, $p = 0.80$).

A. hudsonica frequently reversed the direction of movement of its appendages while feeding, without a consistent pattern (Table S3, Movie S1). This switching movement was not affected by temperature/viscosity or dietary treatment (temperature/viscosity treatment and diet analyzed as a single factor; Pearson's $\chi^2 = 17.88$, $df = 16$, $p = 0.33$). When appendage movement direction was included in the factorial ANOVA, movement direction did have a statistically significant effect on appendage beating frequency ($F_{2,340} = 40.82$, $p < 1\times10^{-7}$), but the interpretation of temperature/viscosity treatment and diet was unchanged (temperature/viscosity: $F_{2,340} = 106.26$, $p < 1\times10^{-7}$ and same Tukey's results; diet: $F_{2,340} = 8.25$, $p = 8.32\times10^{-4}$ and copepods feeding on *T. weissflogii* without tracking particles beating their appendages more slowly than the other two diets). Therefore, we do not distinguish between movement direction in our analysis of appendage beating frequency. The movement direction was sometimes difficult to classify; 12 videos were re-analyzed for consistency, and 18% of appendage movements were classified differently from the original. *Parvocalanus crassirostris* only exhibited appendage reversal when rejecting large particles, and these events were not included in the calculation of appendage beating frequency.

Proportion of time spent swimming

A. hudsonica spent 7.9 - 19.7 % of the time swimming (Fig. 3). The proportion of time spent swimming was affected by temperature/viscosity treatment (ANCOVA, $F_{2,275} = 6.42$, $p = 1.9\times10^{-3}$). Copepods spent 27 - 41 % less time swimming when the viscosity was higher, regardless of temperature (Tukey's post-hoc following ANCOVA, $p < 0.05$). Diet did not affect the proportion of time spent swimming (ANCOVA, $F_{2,275} = 0.78$, $p = 0.46$), and there was no interaction between temperature/viscosity treatment and diet (ANCOVA, $F_{4,275} = 1.85$, $p = 0.12$).

P. crassirostris spent 57.9 - 90.8 % of the time swimming (Fig. 3). The proportion of time spent swimming was not affected by temperature/viscosity treatment (ANCOVA, $F_{2,225} = 1.32$, $p = 0.27$) or diet (ANCOVA, $F_{2,225} = 0.29$, $p = 0.75$), though the interaction was statistically significant (ANCOVA, $F_{4,225} = 2.77$, $p = 0.028$).

A random selection of 12 *P. crassirostris* and 12 *A. hudsonica* videos were re-checked, which showed that proportion of time swimming was consistently and repeatably recorded in the videos (paired t-test, *A. hudsonica*: $t_{11} = -0.95$, $p = 0.36$; *P. crassirostris*: $t_{11} = -1.60$, $p = 0.14$).

Swimming speed

Acartia hudsonica swimming speeds were generally 2 - 4 mm s^{-1} (Fig. 4A-C), corresponding to *Re* of 1 - 3. *Parvocalanus crassirostris* swimming speeds were generally 0.4 - 0.6 mm s^{-1} (Fig. 4D-F), corresponding to *Re* of 0.1 - 0.5. In five out of the six species-orientation combinations, there was a dietary effect on copepod swimming speed, with copepods feeding on *T. weissflogii* swimming more slowly than copepods feeding on *P. minimum* (Fig. 4, Table 4). *Acartia hudsonica* swimming was sometimes slowed by high viscosity, while *P. crassirostris* swimming was sometimes slowed by cold temperature (Table 4).

Discussion

The observed movements of the two copepod species clearly differed, with *P. crassirostris* swimming steadily, while *A. hudsonica* had short active feeding periods. The *A. hudsonica* movement patterns match those observed in an *Acartia* congener (Kiørboe *et al.*, 1996), while the *P. crassirostris* movement patterns consisted of more continuous swimming than previously observed (Bradley *et al.*, 2013).

Based on the differences in their movements, these copepod species may therefore target different prey species and be targeted themselves by different predators; copepods with continuous-swimming movement strategies are more susceptible to predation compared to copepods that use an ambush strategy (van Someren Gréve *et al.*, 2017). Additionally, the swimming and feeding flux of these two copepod species was impacted very differently by changes in temperature and viscosity, with *A. hudsonica* being affected by viscosity while *P. crassirostris* was unaffected.

Our hypotheses about the effects of seawater viscosity on copepod movements were partially upheld. *A. hudsonica* feeding flux was reduced by high viscosity but not temperature, and *P. crassirostris* feeding flux was not affected by either temperature or viscosity (Table 2). Similarly, high viscosity reduced the number of *A. hudsonica* twitches, possibly indicating a reduction in particle capture, while *P. crassirostris* twitching was not affected by treatment (Tables 1, 3). Furthermore, *A. hudsonica* swimming time and swimming speed were both reduced by high viscosity, while *P. crassirostris* was not affected (Figs. 3-4, Table 4). Correspondingly, feeding of the congener *A. tonsa* is severely reduced by increased seawater viscosity, and *P. crassirostris* feeding is less sensitive to viscosity (Tyrell and Fisher, 2019). Rather than reducing *P. crassirostris* feeding flux, high seawater viscosity may diminish particle capture efficiency (Koehl, 1981), thus explaining reduced feeding at high viscosity (Tyrell and Fisher, 2019). Therefore, our hypothesis that temperature effects can be explained by viscosity was partially supported by the data. However, our hypothesis that *A. hudsonica* would be less sensitive to viscosity due to its more northward range was not supported. Future research should broadly investigate other copepod and zooplankton species to determine how they respond to changes in seawater viscosity and temperature and whether latitudinal and feeding-mechanism-specific response patterns exist.

Both *A. hudsonica* and *P. crassirostris* cleared volumes similar to the 10^6 body volumes per day required to satisfy energetic requirements (Kiørboe, 2011; Kiørboe and Jiang, 2013), and *A. hudsonica* clearance rates match previous measurements of its congener *A. tonsa* (Kiørboe et al., 1996) (Table 2). *Parvocalanus crassirostris* clears slightly more body volumes of water per day than *A. hudsonica*; this higher clearance rate is reflected in a higher respiration per unit body volume (Tyrell et al., in review).

To our knowledge, we are the first to use the Python libraries *OpenCV2* and *trackpy* to track fluid flow around zooplankton, although other groups have used these libraries in different contexts (Bianco et al., 2013; Urmy and Warren, 2017; Wolf and Heuschele, 2018). These libraries offer an open-source alternative fluid analysis method that works even under conditions when Particle Image Velocimetry (PIV) analysis is not suitable due to low particle densities, and we encourage future work to use *OpenCV2* and *trackpy* to track fluid flow.

Increases in seawater viscosity reduced *A. hudsonica* swimming speed by 23 - 28 % in limited cases (Table 4), compared to previous studies showing a 50% decrease in swimming speed over a comparable viscosity range (Larsen et al., 2008). *Acartia hudsonica* swimming speeds of 2 - 4 mm s^{-1} (Fig. 4A-C) match previously published speeds of *Acartia* spp. (Buskey et al., 1983; Larsen et al., 2008). In contrast, there was no effect of viscosity on *P. crassirostris* swimming speed, though cold temperature sometimes caused a 25 - 26 % decrease in swimming speed (Table 4). *Parvocalanus crassirostris* speeds near 0.5 mm s^{-1} (Fig. 4D-F) are similar to previous studies (Bradley et al., 2013).

A viscous speed response may have been masked or diminished due to the relatively high cell densities. Copepod swimming speeds slow at a cell density of 10^4 - 10^5 cells mL^{-1} (van Duren and Videler, 1995), which is the range of cell densities used in our study. We chose a high density of copepods with a high cell density to maximize the number of videos while ensuring that the copepods would have sufficient cells remaining after an acclimation period. Future video studies could investigate the effect of seawater viscosity and temperature on copepod swimming speeds at lower cell densities.

The measured percent of time that *A. hudsonica* spent swimming was low (7.9 - 19.7 %) (Fig. 2) compared to a previous study that reported up to 40% active swimming time in a congener (Kiørboe et al., 1996). Previous study has been limited to frame rates as low as 30 - 50 frames s^{-1} (0.02 - 0.03 s $frame^{-1}$) (Kiørboe et al., 1996; Turner et al., 1993), which could cause multiple short periods to be classified as one longer period, thereby artificially inflating the measured active swimming time. The percent of time that *P. crassirostris* spent swimming (57.9 - 90.8 %) was higher than the 33% previously reported (Bradley et al., 2013).

Overall, *P. crassirostris*'s lack of viscous response may lead to more energy being spent at high viscosities and cold temperatures, while *A. husonica*'s reduction in swimming speed and activity at high viscosity and cold temperature may result in less energy being spent. However,

the total amount of energy spent on movement is generally < 2% of the total metabolic rate (Vlyman, 1970; Kiørboe *et al.*, 1985; van Duren and Videler, 2003), so this difference in response may instead stem from differing muscle strengths or sensitivity to stimuli rather than from an energy conservation requirement. Furthermore, a sensitivity to seawater viscosity may not necessarily propagate into ecological effects if the growth, reproduction, and survival of the copepod is not affected. When considering the energetic balance of ingestion and respiration, the *A. hudsonica* congener *A. tonsa* has optimal temperatures lower than those of *P. crassirostris* (Tyrell et al., in press), and *A. hudsonica* is found at colder temperatures than *P. crassirostris* (Lonsdale and Coull, 1977; Sullivan et al., 2007), indicating that *A. hudsonica* is more adapted to cold environments than *P. crassirostris*. Future research should investigate these issues, as well as investigating how temperature-related differences in movement, such as the *A. hudsonica* reduction in proportion of time spent swimming and swimming speed, translate to ecological impacts on predation and reproduction; less movement of *A. hudsonica* at colder temperatures may result in less predation under these conditions.

The distinct physiological effect of temperature on copepod appendage beating (Fig. 2) was not reflected in any temperature effect on copepod movements, activity, feeding flux, or swimming speed of *A. hudsonica*, though *P. crassirostris* swimming speed was sometimes reduced by cold temperature (Fig. 4, Table 4). The lack of a viscous response is unexpected, given that an appendage has a maximum *Re* of approximately 1 (Cheer and Koehl, 1987), which implies that changes in viscosity should affect movement. The mechanisms that control copepod appendage movement are conserved across life stages, as previous data on copepod nauplii show similar results (Gemmell *et al.*, 2013). Our results match the pattern of larger copepods having slower appendage beating frequencies (Price and Paffenhofer, 1986; Dagg and Wasler, 1986); *A. hudsonica* (0.8 mm cephalothorax length) had a slower appendage beating frequency than *P. crassirostris* (0.35 mm cephalothorax length) (Fig. 2). *Parvocalanus crassirostris* appendage beating frequency was more severely reduced by cold temperature compared to *A. hudsonica* (Fig. 2). *Acartia hudsonica* has amyelinated nerves, while *P. crassirostris* has myelinated nerves (Buskey et al., 2017). Myelinated nerves respond more quickly to stimuli (Buskey et al., 2017; Lenz et al., 2000) but are more sensitive to low temperatures (Franz and Iggo, 1968). Based off of copepod reaction times (2 - 10 ms) (Waggett and Buskey, 2008), copepod nerves transmit at 100 - 500 Hz, compared to appendage beating frequencies of 12 - 75 Hz; a temperature-induced

reduction in nerve transmission speed of 3x (Franz and Iggo, 1968) would reduce nerve transmissions to 30 - 170 Hz, possibly lowering nerve transmission frequency below optimal appendage beating frequency and thereby slowing appendage beating.

Most copepod movements were not affected by diet, contrary to our hypothesis. In contrast to the temperature/viscosity treatment, the diet treatment did not affect copepod swimming time (Fig. 2) or movements (Tables 1-2), or appendage beating frequency of *P. crassirostris* (Fig. 2), although the appendage beating frequency of *A. hudsonica* was increased when feeding on *T. weissflogii* with tracking particles added compared to when feeding on *T. weissflogii* without tracking particles (Fig. 2). This may reflect an influence of the particle size on the appendage beating frequency, as the tracking particles were smaller than the algal cells (3μm diameter compared to ~10 – 20 μm diameter). This lack of behavioral response to diet contrasts with some recent findings that showed that food quality impacts behavior (Herstoff *et al.*, 2019); though it is likely that both diets were nutritionally replete. Copepods prefer motile prey over non-motile prey (Atkinson, 1996; Verity and Paffenhofer, 1996)) and tend to have higher ingestion rates when feeding on motile prey (Jakobsen *et al.*, 2005, Henriksen *et al.*, 2007). Future study should investigate the movements and swimming speeds associated with selectivity when feeding on multi-algal diets of differing nutritional quality.

Diet distinctly impacted copepod swimming speeds, with copepods feeding on *T. weissflogii* consistently swimming 22 - 39 % more slowly than copepods feeding on *P. minimum* (Fig. 4, Table 4). Changes in swimming speed may serve to maximize capture efficiency depending on cell characteristics (Koehl, 1981). This diet-induced change in swimming speed may propagate into ecosystem-level effects, as swimming speed influences both mating (Kiørboe and Bagoien, 2005) and risk of predation (Buskey, 1994; van Someren Gréve et al., 2017), and ecological models should be used to investigate these endpoints.

Conclusions

The swimming speeds and behaviors of two copepod species were influenced by both temperature and viscosity in different and biologically meaningful ways. Notably, only *A. hudsonica* responded to increased seawater viscosity. These distinct behaviors highlight the diversity of the zooplankton movement strategies and the differing ways that zooplankton respond to environmental conditions. A better understanding of calanoid feeding and movement

behavior may help explain copepod distributions and trophic interactions. Broadly, the individual-level details resolved in videography studies are an important contribution to our understanding of marine zooplankton ecology; videography studies should be expanded to include more copepod and zooplankton species. Future study should also investigate latitudinal patterns in copepod feeding mechanisms to determine how seawater viscosity and temperature may have influenced the evolution and development of different feeding mechanisms.

Acknowledgements

We thank P. Alatalo, S. Baines, N. Chatterjee, B. Colon, T. Gaylor, E. Herstoff, J. Kraemer, Y. C. Lu, M. Mace, B. Michel, V. Mikros, M. Niemisto, J. Padilla, N. Tyrell, and L. Wong for assistance.

Competing interests

No competing interests declared.

Funding

This study was supported by the National Science Foundation [OCE1634024 to N.F.; OCE-1433979 and OCE-1559062 to H.J.]; and by Stony Brook University [Graduate Council Fellowship and Turner Fellowship to A.S.T].

Data availability

Data are archived at the Stony Brook University Library Academic Commons, indexed under the School of Marine and Atmospheric Sciences.

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Figures

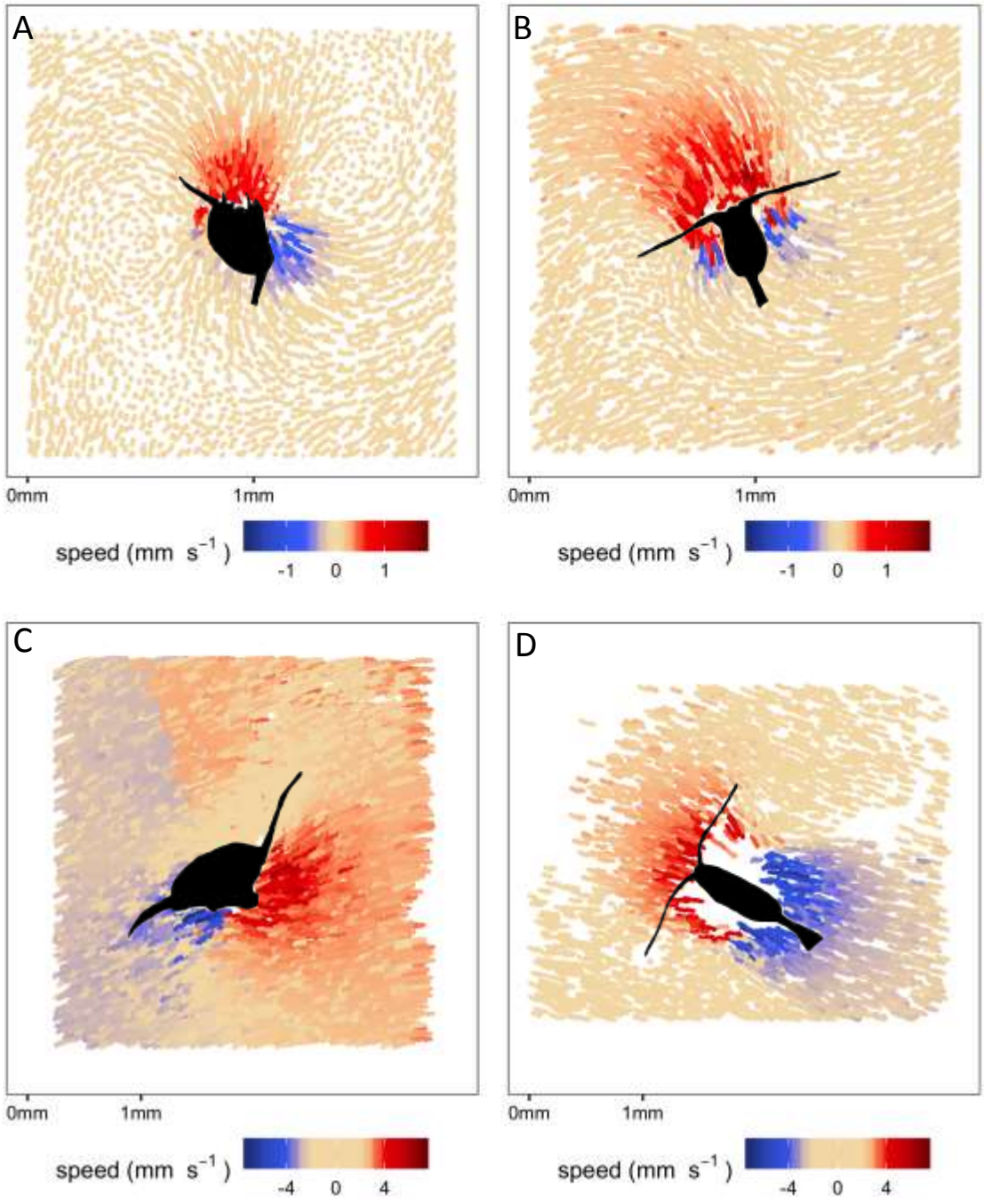


Figure 1. Speed and tracks of particles around swimming copepods: a *Parvocalanus crassitostris* female from a sagittal ("side") view (A), and a *Parvocalanus crassitostris* female from a dorsoventral ("top") view (B), an *Acartia hudsonica* female from a sagittal ("side") view (C), an *Acartia hudsonica* female from dorsoventral ("top") view (D). Particles are colored according to whether they were moving towards (red) or away from (blue) the center of the

copepod. Intensity of color indicates the magnitude of the particle speed as shown in scales; note differing scale for each panel. The field of view is 400x400 pixel (A, B) or 800x800 pixel (C, D). All videos had tracking particles added to the seawater. Particles were tracked over 0.5 s (A, B), 0.13 s (C), or 0.05 s (D). Videos were taken at 10^{o}C (A, B), or 20^{o}C (C, D). The particle trajectories are centered on the copepod's movement.

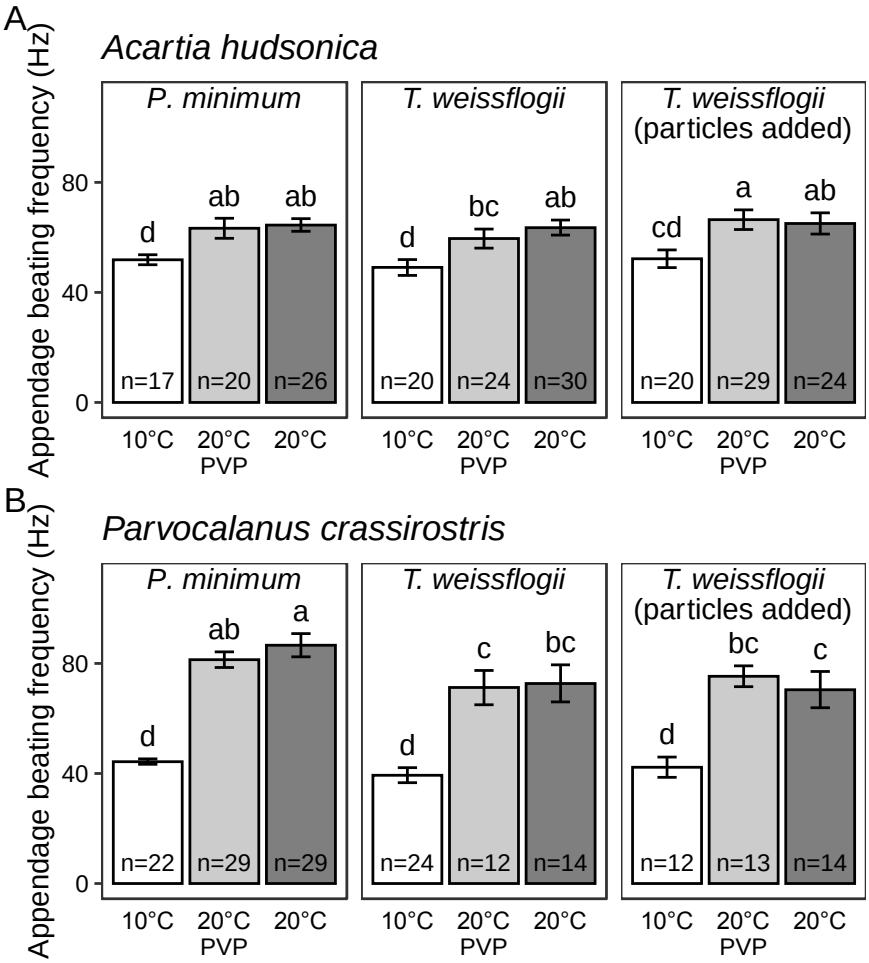


Figure 2. *Acartia hudsonica* (A) and *Parvocalanus crassirostris* (B) appendage beating frequency. Feeding on *Prorocentrum minimum* or *Thalassiosira weissflogii* with or without tracking particles (as labelled on graph). Measurements taken at 10°C (white), 20°C with high viscosity (light gray), or 20°C (dark gray). Sample sizes are shown on graph; each measurement came from one copepod. Error bars represent ±2SE. Letters show significance of pairwise comparison (Tukey's HSD following two-factor ANOVA, $p < 0.05$).

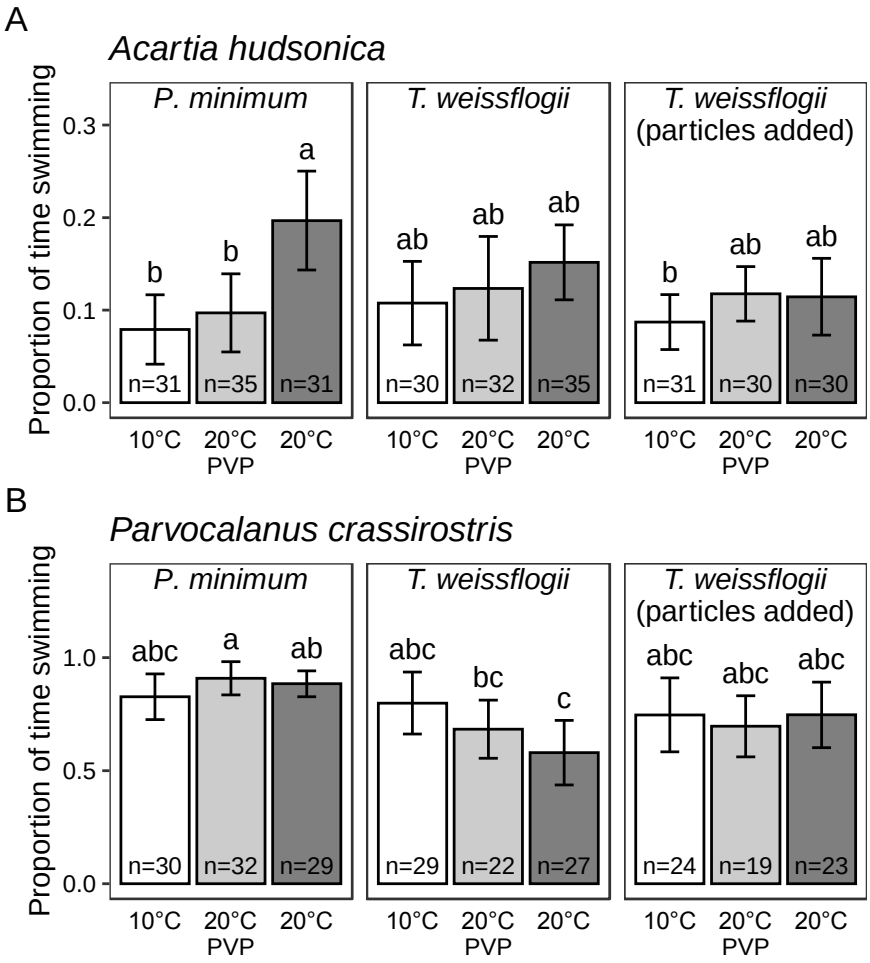


Figure 3. Proportion of time spent swimming by *Acartia hudsonica* (A) and *Parvocalanus crassirostris* (B). Measurements taken at 10ºC (white), 20ºC with high viscosity (light gray), or 20ºC (dark gray). Feeding on *Prorocentrum minimum* or *Thalassiosira weissflogii* with or without tracking particles (as labelled on graph). Sample sizes are shown on graph; each measurement came from one copepod. Error bars represent mean ±2SE. Letters show significance of pairwise comparison (Tukey's HSD following two-factor ANOVA, $p < 0.05$).

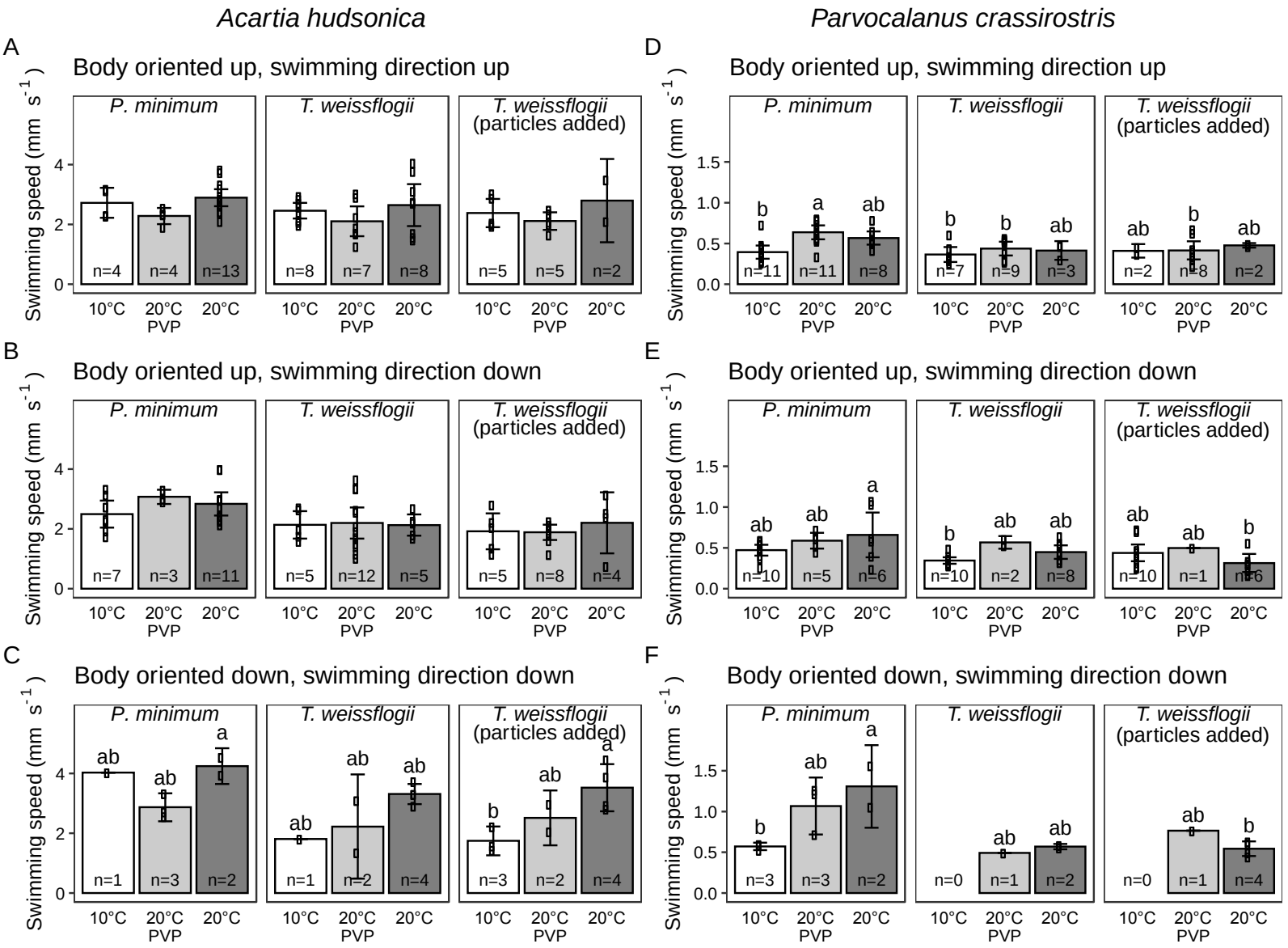


Figure 4. Swimming speeds of *Acartia hudsonica* (A-C) and *Parvocalanus crassirostris* (D-F). The orientation of the copepod and its displacement direction are indicated on the figure. Note differing y scales for each species. Measurements taken at 10°C (white), 20°C with high viscosity (light gray), or 20°C (dark gray). Feeding on *Prorocentrum minimum* or *Thalassiosira weissflogii* with or without tracking particles (as labelled on graph). Sample sizes are shown on graph; points show individual measurements, each of which came from one copepod. Error bars represent mean ±2SE. Letters show significance of pairwise comparison within groups with the same body orientation and swimming direction (Tukey's HSD following two-factor ANOVA, $p < 0.05$). Lack of letters indicates no pairwise differences. Detailed statistical results are shown in Table 4.

Tables

Species	Movement	Model family	Parameter	Model comparison[a]	df	χ^2	*p*
A. hudsonica	Twitch while swimming	Negative Binomial	Diet	2 vs 1	2	1.89	0.39
				3 vs 4	2	2.15	0.34
			Treatment[b]	1 vs 3	2	23.90	6.4×10^{-6} *
				3 vs 4	2	24.16	5.6×10^{-6} *
			Interaction	4 vs 5	4	5.42	0.25
	Large hops	Negative Binomial	Diet	2 vs 1	2	3.92	0.14
				3 vs 4	2	3.95	0.14
			Treatment	1 vs 3	2	1.98	0.37
				3 vs 4	2	2.01	0.37
			Interaction	4 vs 5	4	6.56	0.16
	Small hops	Negative Binomial	Diet	2 vs 1	2	0.32	0.85
				3 vs 4	2	0.40	0.82
			Treatment	1 vs 3	2	4.51	0.10
				3 vs 4	2	4.60	0.10
			Interaction	4 vs 5	4	5.19	0.27
	Jump	Negative Binomial	Diet	2 vs 1	2	0.68	0.71
				3 vs 4	2	0.72	0.70
			Treatment	1 vs 3	2	2.83	0.24
				3 vs 4	2	2.87	0.24
			Interaction	4 vs 5	4	8.90	0.064
P. crassirostris	Twitch while swimming	Negative Binomial	Diet	2 vs 1	2	3.37	0.19
				3 vs 4	2	2.97	0.23
			Treatment	1 vs 3	2	3.47	0.18
				3 vs 4	2	3.07	0.21
			Interaction	4 vs 5	4	12.17	0.016
	Large hop	Negative Binomial	Diet	2 vs 1	2	0.98	0.61
				3 vs 4	2	1.02	0.60
			Treatment	1 vs 3	2	0.53	0.77
				3 vs 4	2	0.57	0.75
			Interaction	4 vs 5	4	5.00	0.29
	Jump	Poisson	Diet	2 vs 1	2	4.78	0.09
				3 vs 4	2	4.46	0.11
			Treatment	1 vs 3	2	1.88	0.39

	3 vs 4	2	1.55	0.46
Interaction	4 vs 5	4	7.05	0.13

Table 1. Movement model comparisons. χ^2 Likelihood Ratio Test was used to compare goodness-of-fit of pairs of full and reduced models.

[a] Models: 1: Movement ~ Length (reduced model);

2: Movement ~ Diet + Length;

3: Movement ~ Treatment + Length;

4: Movement ~ Diet + Treatment + Length;

5: Movement ~ Diet * Treatment + Length

[b] Groupwise parameter estimates of zero-intercept single factor model ±2SE (untransformed): 10ºC: -0.74±0.39; 20ºC+PVP: -0.55±0.36; 20ºC: 0.30±0.30. The 20ºC treatment has a statistically higher number of twitches than the other two treatments.

[*] $p < 0.0014$ (Bonferroni-corrected α): reduced model is rejected; full model provides a better fit of the data.

Species	Treatment	Flux (mL day^{-1} copepod^{-1}) ± 2 SE (n)	Flux (10^6 BV day^{-1} copepod^{-1}) ± 2 SE (n)	Percent of time spent swimming[a]	Flux corrected for activity (mL day^{-1} copepod^{-1})	Flux corrected for activity (10^6 BV day^{-1} copepod^{-1})
Acartia	10°C	51.97 (1)	1.42 (1)	9.1	4.73	0.13
hudsonica	20°C+PVP	77.92±29.86 (3)	2.14±0.80 (3)	11.2	8.73	0.24
	20°C	209.66±23.34 (2)	5.68±0.82 (2)	15.5	32.50	0.88
Parvocalanus	10°C	11.88±3.88 (7)	1.95±0.57 (7)	79.4	9.43	1.55
crassirostris	20°C+PVP	10.21±2.10 (5)	1.78±0.45 (5)	78.5	8.01	1.40
	20°C	8.59 (1)	1.90 (1)	74.0	6.36	1.41

Table 2. Summary of copepod feeding flux, with correction for percent of time spent swimming.

[a] Mean percent of time spent swimming across all diets.

Movement	Diet	*A. hudsonica*			*P. crassirostris*		
		Treatment			Treatment		
		10ºC	20ºC+PVP	20ºC	10ºC	20ºC+PVP	20ºC
Number of copepods analyzed	*Prorocentrum minimum*	31	35	32	30	32	29
	Thalassiosira weissflogii	30	32	36	29	19	27
	Thalassiosira weissflogii (tracking particles)	31	30	30	24	19	23
Beats feeding appendages	*Prorocentrum minimum*	0.55	0.57	0.88	0.93	1	1
	Thalassiosira weissflogii	0.67	0.75	0.92	0.90	0.95	0.81
	Thalassiosira weissflogii (tracking particles)	0.71	0.97	0.80	0.83	0.95	0.87
Sink (motionless)	*Prorocentrum minimum*	1	1	1	0.37	0.31	0.48
	Thalassiosira weissflogii	1	1	1	0.10	0.73	0.63
	Thalassiosira weissflogii (tracking particles)	1	1	1	0.25	0.63	0.57
Twitches antenna(e) and/or urosome while swimming	*Prorocentrum minimum*	0.16 (1)	0.31 (1)	0.69 (2)	0.43 (3)	0.69 (2.5)	0.79 (2)
	Thalassiosira weissflogii	0.23 (1)	0.28 (1)	0.53 (2)	0.34 (3)	0.82 (4)	0.48 (2)
	Thalassiosira weissflogii (tracking particles)	0.29 (1)	0.67 (1)	0.40 (1.5)	0.46 (4)	0.53 (2)	0.70 (3)
Small hop[a]	*Prorocentrum minimum*	0.10 (3)	0.26 (1)	0.38 (1)			
	Thalassiosira weissflogii	0.10 (1)	0.47 (1)	0.17 (1)		n/a	
	Thalassiosira weissflogii (tracking particles)	0.13 (1)	0.40 (1)	0.27 (1)			
Large hop[b]	*Prorocentrum minimum*	0.94 (4)	0.94 (3)	0.91 (3)	0.07 (1)	0.06 (1)	0.07 (1)
	Thalassiosira weissflogii	0.83 (3)	0.91 (3)	0.92 (2)	0.14 (1)	0.05 (2)	0.07 (1)
	Thalassiosira weissflogii (tracking particles)	0.97 (3)	0.97 (3)	0.97 (2)	0	0.16 (1)	0.04 (1)
Jump[c]	*Prorocentrum minimum*	0.06 (1.5)	0.06 (1)	0	0.27 (1)	0.22 (1)	0.52 (1)
	Thalassiosira weissflogii	0.07 (1)	0.13 (1)	0.06 (1)	0.24 (1)	0.41 (1)	0.30 (1)
	Thalassiosira weissflogii (tracking particles)	0.10 (2)	0	0	0.21 (1)	0.21 (1)	0.35 (1)

Table 3. Movement summary of *Acartia hudsonica* and *Parvocalanus crassirostris*: proportion of videos with the specified movement present. Value in parentheses represents the median number of movements in the videos with the movement present.

[a] Incomplete deployment of swimming appendages.

[b] *A. hudsonica*: ≤2 beats of swimming appendages; *P. crassirostris*: ≤3 beats of swimming appendages

[c] *A. hudsonica*: >2 beats of swimming appendages; *P. crassirostris*: >3 beats of swimming appendages

Analysis	Copepod	Body and swimming orientation		
		Body oriented up, swimming direction up	**Body oriented up, swimming direction down**	**Body oriented down, swimming direction down**
Effect of treatment	*A. hudsonica*	Copepods at 20ºC swam 23% slower when viscosity was lower; no other differences ($F_{2,47}$ = 3.94, p = 0.026)	No effect of temperature/ viscosity ($F_{2,51}$ = 0.50, p = 0.61)	Copepods at higher viscosity swam 28-38% slower, regardless of temperature; no other differences ($F_{2,13}$ = 11.58, p = 1.3×10^{-3})
	P. crassirostris	Copepods at 10ºC swam 25-26% slower than other treatments; no other differences ($F_{2,52}$ = 7.51, p = 1.4×10^{-3})	No effect of temperature/viscosity ($F_{2,49}$ = 1.93, p = 0.15)	Effect of temperature/viscosity, but no groupwise differences ($F_{2,9}$ = 8.85, p = 7.5×10^{-3})
Effect of diet	*A. hudsonica*	No effect of diet ($F_{2,47}$ = 0.83, p = 0.44)	Copepods feeding on *T. weissflogii* swam 24% slower than copepods feeding on *P. minimum* ($F_{2,51}$ = 6.28, p = 3.6×10^{-3})	Copepods feeding on *T. weissflogii* swam 22% slower than copepods feeding on *P. minimum* ($F_{2,13}$ = 5.10, p = 0.023)
	P. crassirostris	Copepods feeding on *T. weissflogii* swam 22% slower than copepods feeding on *P. minimum* ($F_{2,52}$ = 7.21, p = 1.7×10^{-3})	Copepods feeding on *T. weissflogii* swam 27% slower than copepods feeding on *P. minimum* ($F_{2,49}$ = 4.97, p = 0.011)	Copepods feeding on *T. weissflogii* swam 39% slower than copepods feeding on *P. minimum* ($F_{2,9}$ = 13.58, p = 1.9×10^{-3})
Effect of interaction	*A. hudsonica*	Not significant ($F_{4,47}$ = 0.05, p = 0.99)	Not significant ($F_{4,51}$ = 0.40, p = 0.81)	Not significant ($F_{4,13}$ = 1.23, p = 0.35)
	P. crassirostris	Not significant ($F_{4,52}$ = 1.66, p = 0.17)	Not significant ($F_{4,49}$ = 2.28, p = 0.07)	Not significant ($F_{2,9}$ = 1.36, p = 0.30)

Table 4. Detailed statistical summary of effects of temperature/viscosity and diet on copepod swimming speed. Copepod swimming speed for each body and swimming orientation was analyzed by two-factor ANOVA with Type III error with diet and temperature/viscosity treatment as co-factors. Results of ANOVAs are in parentheses. Groupwise differences were determined by Tukey's post-hoc test with a significance level set at $p < 0.05$. Significance of pairwise comparisons are shown in Fig. 4.

Movie 1

Example of *Acartia hudsonica* swimming, with switching of appendage movement direction. Playback is at 20 frames per second (100x slower than real time). The copepod was in the 10ºC treatment, feeding on *Thalassiosira weissflogii* with no tracking particles.

Movie 2

Example of *Acartia hudsonica* swimming, with antenna twitches. Playback is at 20 frames per second (100x slower than real time). The copepod was in the 10ºC treatment, feeding on *Thalassiosira weissflogii* with no tracking particles.

Movie 3

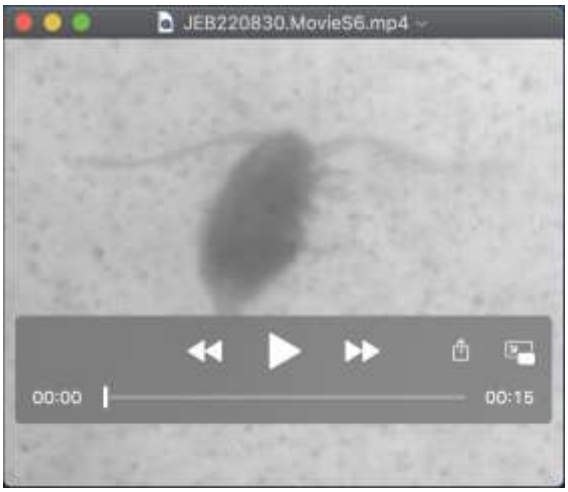
Example of an *Acartia hudsonica* large hop. Playback is at 20 frames per second (100x slower than real time). The copepod was in the 10ºC treatment, feeding on *Thalassiosira weissflogii* with no tracking particles.

Movie 4

Example of *Parvocalanus crassirostris* swimming. Playback is at 20 frames per second (100x slower than real time). The copepod was in the 10ºC treatment, feeding on *Thalassiosira weissflogii* with tracking particles.

Movie 5

Example of *Parvocalanus crassirostris* swimming, with twitching of the urosome. Playback is at 20 frames per second (100x slower than real time). The copepod was in the 10ºC treatment, feeding on *Thalassiosira weissflogii* with tracking particles.



Movie 6

Example of a *Parvocalanus crassirostris* jump. Playback is at 20 frames per second (100x slower than real time). The copepod was in the 10ºC treatment, feeding on *Thalassiosira weissflogii* with tracking particles.

Date	Copepod species	Diet species	Temperature (ºC)	Viscosity ($\times10^{-3}$ kg m^{-1} s^{-1})	Starting cell density ±SD (tracking particle density ±SD) ($\times10^{4}$ mL^{-1}) [a]	Ending cell density ±SD (tracking particle density ±SD) ($\times10^{4}$ mL^{-1}) [a]	Mean cephalothorax length (mm) ± 2 SE (n) [b]	Mortality check [c]
5/17/2018	*Parvocalanus crassirostris*	*Thalassiosira weissflogii*	10	1.416	2.5±0.7 (0)	1.6±0.1 (0)	0.368±0.011 (18)	55 alive females 3 alive males 1 molt
5/18/2018	*Parvocalanus crassirostris*	*Thalassiosira weissflogii*	10	1.406	1.0±0.8 (287.5±24.7)	0.8±0.3 (310±28.3)	0.373±0.025 (9)	55 alive females 4 dead 1 molt
5/22/2018	*Parvocalanus crassirostris*	*Prorocentrum minimum*	10	1.415[c]	1.2±0 (0)	1.1±0.1 (0)	0.394±0.014 (15)	62 alive females 2 alive males 2 alive copepodites 1 molt
5/23/2018	*Acartia hudsonica*	*Thalassiosira weissflogii*	10	1.405	12.8±0.3 (0)	13.1±1.3 (0)	0.763±0.021 (21)	47 alive females 1 alive male 6 motionless
5/24/2018	*Acartia hudsonica*	*Prorocentrum minimum*	10	1.405	10.7±3.3 (0)	9.4±1.4 (0)	0.784±0.017 (20)	55 alive females 1 dead
5/25/2018	*Acartia hudsonica*	*Thalassiosira weissflogii*	10	1.411	Flask 1: 11.7±1.8 (75.0±14.1) Flask 2: 14.1±0.4 (116.3±8.8)	Flask 1: 9.1±0.1 (62.5±10.6) Flask 2: 10.8±2.0 (86.3±5.3)	Flask 1: 0.720±0.125 (8) Flask 2: 0.784±0.023 (12)	Flask 1: 29 alive females 1 motionless 1 copepodite Flask 2: 29 alive females
5/31/2018	*Parvocalanus crassirostris*	*Thalassiosira weissflogii*	20	1.104	2.2±0.3 (0)	1.3±0.4 (0)	0.348±0.023 (6)	56 alive females 2 motionless 1 dead 1 alive male

5/31/2018	*Parvocalanus crassirostris*	*Thalassiosira weissflogii*	20	1.104	1.4±0.3 (202.5±24.7)	1.4±0.6 (190.0±28.3)	0.353±0.027 (10)	58 alive females 2 alive males
6/1/2018	*Parvocalanus crassirostris*	*Thalassiosira weissflogii*	20	1.328	1.7±0.4 (0)	1.0±0 (0)	0.363±0.027 (8)	47 alive females 1 dead 10 alive males
6/1/2018	*Parvocalanus crassirostris*	*Thalassiosira weissflogii*	20	1.328	1.2±0.3 (132.5±31.8)	1.5±0.1 (167.5±3.5)	0.359±0.024 (12)	40 alive females 7 dead 1 motionless 10 alive males
6/5/2018	*Parvocalanus crassirostris*	*Prorocentrum minimum*	20	1.109	1.1±0.4 (0)	1.8±0 (0)	0.378±0.011 (12)	55 alive females 2 dead 1 alive male
6/6/2018	*Parvocalanus crassirostris*	*Prorocentrum minimum*	20	1.324	0.6±0.5 (0)	0.8±0.1 (0)	0.380±0.009 (20)	59 alive females 1 alive male
6/7/2018	*Acartia hudsonica*	*Prorocentrum minimum*	20	1.102[d]	12.0±1.4 (0)	11.6±1.4 (0)	0.788±0.018 (22)	45 alive females 14 dead females 1 motionless female
6/8/2018	*Acartia hudsonica*	*Thalassiosira weissflogii*	20	1.093	4.8±1.4 (0)	4.6±1.7 (0)	0.793±0.015 (22)	42 alive females 11 dead females 2 dead males 2 alive males
6/12/2018	*Acartia hudsonica*	*Prorocentrum minimum*	20	1.351	11.3±0.7 (0)	11.6±1.1 (0)	0.787±0.017 (25)	44 alive females 15 dead females 1 alive male
6/19/2018	*Acartia hudsonica*	*Thalassiosira weissflogii*	20	1.374	20.2±2.5 (0)	20.7±0.4 (0)	0.777±0.017 (20)	50 alive females 9 dead females 1 alive male
6/20/2018	*Acartia hudsonica*	*Thalassiosira weissflogii*	20	1.102	Flask 1: 11.4±2.3 (87.5±10.6)	Flask 1: 10.7±1.3 (85.0±14.1)	Flask 1: 0.802±0.025 (6)	Flask 1: 22 alive females 6 dead females

					Flask 2: 14.4±0.6 (80.0±21.1)	Flask 2: 9.4±2.3 (90.0±28.3)	Flask 2: 0.770±0.017 (12)	Flask 2: 24 alive females 5 dead females
6/20/2018	*Acartia hudsonica*	*Thalassiosira weissflogii*	20	1.347	Flask 1: 8.1±2.4 (120.0±21.2) Flask 2: 7.2±2.3 (105.0±7.1)	Flask 1: 10.4±1.4 (87.5±17.7) Flask 2: 10.3±1.3 (82.5±38.9)	Flask 1: 0.796±0.017 (8) Flask 2: 0.798±0.020 (9)	Flask 1: 26 alive females 2 dead females 2 alive males 1 molt Flask 2: 23 alive females 4 dead females 1 alive male

Table S1. Summary of conditions during copepod videos. *Acartia hudsonica* was in 40 mL of seawater, and *Parvocalaus crassirostris* was in 20 mL of seawater.

[a] Calculated from two haemocytometer counts.

[b] Size was measured from videos, so n is less than the total number of copepods in the flask.

[c] Counted at end of video period. “Motionless” indicates copepods that were not conclusively alive or dead. Sex of dead copepods is specified when possible to distinguish.

[d] Missing seawater sample for viscosity; substituted average of all other measurements of the same treatment.

Program	General purpose	Package	Version	Link
R (version 3.6.1 (2019-07-05))	Graphics	ggplot2	3.2.0	https://CRAN.R-project.org/package=ggplot2
		ggpubr	0.2.1	https://CRAN.R-project.org/package=ggpubr
		grDevices	3.6.1	Base package
	Copepod movement analysis	MuMIn	1.43.6	https://CRAN.R-project.org/package=MuMIn
		MASS	7.3-51.4	https://CRAN.R-project.org/package=MASS
		lazyeval	0.2.2	https://CRAN.R-project.org/package=lazyeval
	Statistics (ANOVA, ANCOVA, Tukey's post-hoc test, t-test, likelihood ratio test, chi-square test)	multcompView	0.1-7	https://CRAN.R-project.org/package=multcompView
		stats	3.6.1	Base package
		car	3.0-3	https://CRAN.R-project.org/package=car
	Data processing/ visualization	dplyr	0.8.3	https://CRAN.R-project.org/package=dplyr
		knitr	1.23	https://CRAN.R-project.org/package=knitr
		readxl	1.3.1	https://CRAN.R-project.org/package=readxl
		utils	3.6.1	Base package
	Particle tracking analysis	ggplot2	3.2.1	https://CRAN.R-project.org/package=ggplot2
		stringr	1.4.0	https://CRAN.R-project.org/package=stringr
		foreach	1.4.7	https://CRAN.R-project.org/package=foreach
		doParallel	1.0.15	https://CRAN.R-project.org/package=doParallel
		plot3D	1.3	https://CRAN.R-project.org/package=plot3D
Python 2.7.17 (Anaconda, Inc)	Particle tracking analysis	numpy	1.16.1	https://pypi.org/project/numpy/
		pandas	0.24.1	https://pypi.org/project/pandas/
		opencv-python	4.1.2.30	https://pypi.org/project/opencv-python/
		trackpy	0.4.1	https://pypi.org/project/trackpy/0.2.4/
		matplotlib	2.2.3	https://pypi.org/project/matplotlib/

Table S2. Summary of software and major packages used in data processing, analysis, and visualization.

Diet	Movement	10ºC	20ºC+PVP	20ºC
Prorocentrum minimum	Forward	51.7±2.7 (13)	57.6±3.7 (12)	62.4±2.6 (22)
	Backwards	53.3±3.6 (8)	67.3±6.6 (7)	67.2±7.0 (10)
	Both	53.6±4.0(6)	67.4±5.0 (14)	69.4±5.9 (15)
	Unknown	45.1 (1)	64.9±7.4 (4)	-
Thalassiosira weissflogii	Forward	43.1±2.2 (9)	54.1±4.6 (11)	59.6±3.7 (20)
	Backwards	47.0±2.7 (13)	58.5±3.8 (18)	64.8±4.1 (12)
	Both	52.1±2.9 (15)	66.0±4.7 (14)	69.9±3.9 (19)
	Unknown	-	44.1 (1)	61.6±4.9 (9)
Thalassiosira weissflogii (tracking particles)	Forward	50.1±3.6 (10)	59.7±5.7 (18)	60.1±4.4 (19)
	Backwards	53.1±8.4 (9)	64.3±3.9 (15)	65.1±5.3 (8)
	Both	53.2±3.4 (16)	71.7±3.4 (22)	72.6±4.3 (12)
	Unknown	-	52.6 (1)	60.4±9.0 (4)

Table S3. *Acartia hudsonica* appendage beating frequency, divided by appendage movement direction. Mean appendage beating frequency ±2SE. Numbers in parentheses represent the number of observations.