



Seasonal analysis of *Daphnia pulicaria* swimming behavior

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Key words: Swimming behavior, Stokes' law, food temperature, seasonality, sinking

Abstract

Our study documents individual swimming behavior of *Daphnia pulicaria* over a yearly cycle in a temperate lake. We collected *D. pulicaria*, a common freshwater zooplankton, from Lake Mendota on 10 dates between July 1994 and June 1995 from two depths, 2 m and 10 m. The *Daphnia* were rushed to the laboratory and video-taped as they swam in lake water under lake-ambient temperature and light conditions. Five-second swimming tracks of individual *Daphnia* were filmed and digitized using a motion analysis system. We measured average turning angle, swimming speed and sinking rate for each track. *D. pulicaria* swimming behavior varied over the annual cycle. We found significant differences in turning angle between depths and among months. Sinking rate and swimming speed were significantly different among months but not depths. Sinking rate and swimming speed were not significantly correlated with water temperature. Our results were contrary to Stokes' Law predictions, in that *D. pulicaria* had the slowest sinking speed in June, not in the winter when water temperatures were lowest and viscosity was highest. Body length was significantly correlated with all three swimming variables. We also studied swimming behavior in clonal populations of *D. pulicaria* in different concentrations of the alga, *Chlamydomonas reinhardtii*. *D. pulicaria* did not change swimming speed, turning angle or sinking rate over a range of food concentrations. Finally, swimming behavior in a *D. pulicaria* clone, tested at two temperatures in the laboratory, confirmed the results from our seasonal study; *Daphnia* did not sink as predicted by changes in viscosity.

Introduction

Seasonality is a major component of the changing biotic and abiotic factors with which organisms must cope to survive (Sommer et al., 1986). In the lake environment temperature, food concentration, predation intensity and light levels dramatically change with each season. *Daphnia* are common and abundant organisms in freshwater temperate systems, living in lakes over a range of biotic and abiotic conditions.

Daphnia have become a model system for addressing a wide range of ecological and evolutionary questions. Much is known about the biology of *Daphnia* and their life history (reviewed in Peters & DeBernardi, 1987), responses to chemical cues (Larsson & Dodson, 1993; Tollrian & Dodson, 1998) and population behaviors, such as diel vertical migration (DeMeester et al., 1998). Recently, individual swimming behavioral patterns in *Daphnia* have been

studied in relation to temperature (Gorski & Dodson, 1996), food and light (Dodson et al., 1997; Larsson & Kleiven, 1995), and the effects of predation risk on swimming behavior (Dodson, 1989). These studies have used clonal populations of *Daphnia* raised in the laboratory.

Unlike populations of clonal, jar-raised *Daphnia*, natural populations experience a wide range of abiotic and biotic conditions. In Lake Mendota, Wisconsin (USA), a temperate eutrophic lake, temperature varies seasonally and with depth. Lake Mendota water temperatures fluctuate between 0 and 25 °C (Brock, 1985) over an annual cycle. The physical properties of water, especially viscosity, change dramatically over this temperature range (Vogel, 1981). For example, water viscosity at 2 °C is about 80% greater than at 25 °C. For small organisms, changes in viscosity can have dramatic impacts on the hydrodynamics of swimming (Vogel, 1981), especially swimming speeds and

Table 1. Summary of Lake Mendota seasonal data. Values given for the three response variables are averages of 12 individuals at a given depth

Date	Julian day	Secchi depth (m)	Sample depth (m)	Water temp (°C)	Body length H (mm)	Swim speed (mm s ⁻¹)	Sink rate (mm s ⁻¹)	Turn. angle (radians)
7/ 7/94		1.1	2	23.5	2.1	7.15	-3.46	1.09
	190		10	23.5	2.1	6.22	-4.08	1.27
8/11/94		1.5	2	23.5	2.1	6.71	-3.67	1.16
			10	23.5	2.1	6.27	-3.20	1.38
	224		20	11.5	2.1	5.99	-3.07	1.37
9/23/94		2.5	2	18.0	2.2	6.50	-3.31	1.30
	265		10		2.2	5.60	-2.96	1.36
10/12/94		2.0	2	16.0	2.1	6.49	-3.00	1.42
	285		10		2.3	7.15	-3.15	1.47
11/11/94		2.8	2	14.0	2.3	6.97	-2.77	1.35
	314		10		2.3	6.70	-2.98	1.46
12/19/94		3.0	2	4.0	2.3	5.72	-2.59	1.47
	353		10	4.0	2.3	6.04	-2.89	1.42
1/24/95	24	ice	2	2.0	2.2	6.15	-2.71	1.39
4/28/95		2.5	2	8.0	2.7	8.11	-4.68	0.99
	118		10		2.2	7.15	-4.29	1.11
5/17/95		3.0	2	12.0	2.6	7.31	-4.90	1.04
	137		10		2.5	6.85	-4.61	1.05
6/27/95		3.5	2	25.0	2.1	5.10	-2.95	1.25
	176		10	18.0	2.1	5.14	-2.51	1.36

sinking rates. Therefore, we predicted that swimming speed and sinking rate would be slower in colder temperatures when viscosity is high. In addition to seasonal fluctuations in water temperature, temperature varies between the epilimnion and hypolimnion of lakes. The range of temperature in Lake Mendota during the period of stratification was 10–25 °C (Table 1). If *Daphnia* do not compensate (behaviorally) for changes in viscosity, Stokes' Law predicts that *Daphnia* will sink slower and swim slower in hypolimnetic temperatures. A simple consideration of metabolic rate, which is strongly influenced by temperature, also predicts slower swimming at lower temperatures. These predictions can be tested by linear regression of sinking and swimming speeds against water temperature.

Biotic factors, such as food and predation, may also be important in altering swimming behavior of individual *Daphnia*. Swimming behavior allows a *Daphnia* to locate food and maintain position in food patches, to swarm and avoid predators. Lake Mendota also experiences large fluctuations in phy-

toplankton abundance (and probably patchiness) and species composition throughout an annual cycle. These changes in phytoplankton distribution and quality may have an effect on swimming behavior (Dodson et al., 1997). In laboratory experiments, Gerritsen and Porter (1982) found no change in *Daphnia magna* swimming speed when individuals were switched between two food concentrations. However, Young & Getty (1987) found that *D. magna* reduces its vertical component of swimming and turns less often in response to increasing food concentration. Cuddington & McCauley (1994) found that *D. pulex* decreased path length (swam slower) when they were in food rich patches. Larsson & Kleiven (1996) have shown that changes in swimming speed in relation to food concentration depend on light regime, and Dodson et al. (1997) have further shown that different species of *Daphnia* display unique swimming responses to different combinations of food concentration and light regime.

Daphnia can locate food faster by swimming fast and in straight lines. Once in a food patch, *Daph-*

nia can remain in the patch by swimming slower and turning more frequently. Thus, using only feeding considerations, we predict that *Daphnia* in a lake will swim fastest during clear water conditions (typical of the winter months and the spring 'clear water phase', and slowest during algal blooms which occur during the summer.

Daphnia are common prey items for many planktivores in Lake Mendota (Johnson, 1995). Individual size and coloration (Zaret, 1980) are important components of prey selection, as well as prey motion. Certain swimming behaviors may increase the conspicuousness of prey to a visual predator, and increased swimming speeds can increase encounter rates with predators (Gerritsen & Strickler, 1977; Dodson, 1972). In predation experiments with rainbow trout (Ware, 1973), prey motion accounted for 19% of the variance in a fish's prey selection. Wright & O'Brien (1982) found fish reacted to moving diaptomid copepods at three times the distance of non-moving prey, and that continuously moving *Daphnia* could be located at significantly greater distances than non-moving copepods. Brewer & Coughlin (1996), using a virtual plankton system, reported that virtual plankton with a higher hopping frequency were preferentially selected by a bluegill sunfish. Using real *Daphnia*, O'Keefe et al. (1998) have shown that bluegill select faster swimming *Daphnia*. Based on the results of these studies of the importance of small-scale behavior in detection by visual predators, we predict that swimming will be modified (e.g. slower speed, decreased turning angle, decreased sinking rate) in environments where predation risk is higher (i.e. well-lit environments).

To test our predictions about swimming behavior, we investigated swimming behavior in a natural population of *Daphnia pulicaria* collected from Lake Mendota. We examined swimming behavior in individuals collected from two depths over many months to test for effects of temperature, food, predation risk and light on swimming behavior. We also quantified *D. pulicaria* swimming behavior under controlled laboratory conditions. We manipulated temperature and tested for differences between two temperatures, 8 and 20 °C. In a second experiment, we maintained consistent temperature and light levels, and tested swimming behavior over a range of food concentrations.

Methods

Multi-factor seasonal study

Sampling

We collected *D. pulicaria* from the deep hole (26 m) in Lake Mendota (43°4'37" N, 89°24'28" W), Dane County, Wisconsin during 10 months in 1994–95. On each sampling day, we measured temperature and dissolved oxygen to find the thermocline and control for differences in temperature among depths sampled. We sampled within the epilimnion at 2 and 10 m with a Schlinder-Patalas trap to collect zooplankton. We transferred samples into clear (2 m) or dark (10 m) jars, stored them in a cooler and immediately returned to the laboratory. Secchi disc measurements were also taken (Table 1). During ice cover *D. pulicaria* populations were extremely low; therefore, we only sampled one date during this period, 7 January 1995. In 9 months we sampled 2 depths, and in August we sampled three depths, 2, 10 and 20 m. In August, we compared swimming behavior in *Daphnia* collected from the hypolimnion at 20 m, and epilimnion at 2 m.

Filming Set-Up

D. pulicaria were videotaped using a mirror and camera arrangement similar to Ramcharan & Sprules (1989) and Gorski & Dodson (1996). In addition, we used a collimated infrared light to avoid variability in behavior caused by different wavelengths of visible light (Smith & Baylor, 1953; Sterns, 1975). Infrared light from light emitting diodes was collimated by double convex lenses (190 mm diameter) and used to create a bright field upon which the *Daphnia* appeared in silhouette. Using four mirrors, we filmed two simultaneous views of the *Daphnia*. Thirty video frame rates were captured per second and five seconds of continuous swimming were recorded for each daphnid.

We filmed *D. pulicaria* under conditions simulating light and temperature levels in Lake Mendota. Twenty-four hours prior to filming, we changed the temperature of the environmental chamber, which houses the filming equipment, to lake epilimnion temperatures, so that *Daphnia* could be filmed at lake temperatures. *D. pulicaria* collected at two meters were filmed under a single overhead light (3.76 $\mu\text{E m}^{-2} \text{s}^{-1}$) to replicate typical light levels occurring at 2 m in Lake Mendota during summer days. *D. pulicaria* collected at 10 m were filmed in complete darkness

using only infrared back-lighting. *D. pulicaria* were filmed in lake water that had been filtered (90 Tm) to remove large particles and copepods, but retain ambient food levels. We haphazardly selected individual *D. pulicaria* from the lake sample, placed them into the video chamber (190 mL) and allowed the daphnid to acclimate to chamber conditions for 2–3 min. After 2–3 min, we began filming until one or more 5 s tracks of continuous swimming were recorded. We filmed 12 individuals collected from each depth. After filming, we measured *D. pulicaria* (top of head to base of spine), and counted eggs in the brood chamber.

Video analysis of swimming behavior of animals taken directly from the lake

We analyzed video images with an ExpertVision motion analysis program as in Gorski & Dodson (1996). Two perpendicular images of a daphnid were filmed simultaneously. The program digitized the motion of the two perpendicular views ($X \times Z$, $Y \times Z$) of a *Daphnia* to create a three dimensional swimming pattern for analysis. We measured and quantified: (i) swimming speed, (ii) sinking rate, and (iii) turning angle. Swimming speed was determined by dividing the total distance moved (sum of displacement between frames) by the duration of the video segment (5 s). This included a mixture of upward swimming and downward sinking episodes. Sinking rate was estimated using the sinking portion of the hop cycle. The negative (downward) changes in vertical coordinates were used to calculate average sinking rates by breaking each hop into positive and negative speeds. For each sequence of negative velocities (in the vertical dimension), we eliminated the first and last speed, and the remaining velocities were averaged. Turning angle was determined by measuring the angle of change of swimming direction from one frame to the next and calculating the average value for the 5 s observation. A small turning angle value indicates relatively straight swimming.

Statistical analysis of video data

Data were tested for ANOVA assumptions of normality, skewness (G1, Sokal & Rohlf, 1981) and homogeneity of variances (Levene's test, Milliken & Johnson, 1992). Swimming speed data were successfully transformed with a reciprocal transformation. However, sinking rate and turning angle did not meet assumption of normality after transformations. Because ANOVA is robust to lack of normality (Sokal &

Rohlf, 1981) and these data satisfied the assumptions of skewness and homogeneity of variances, we used ANOVA and blocked by month to test for differences between depths and among months (Systat, 1992). Three variables were tested (turning angle, swimming speed, and sinking rate), using a Bonferroni corrected p-value to test for significance (Sokal & Rohlf, 1981).

We collected swimming data over a range of temperatures and range of *D. pulicaria* body lengths. To test for relationships, we used OLS regression analyses (Systat, 1992).

Laboratory tests for temperature effects on swimming behavior

We used *D. pulicaria* Lake Mendota clone 1 to test for temperature effects. This clone was started from a female *D. pulicaria* collected from Lake Mendota on 3 September 1993 by P. Dawidowicz and raised in our laboratory on *Chlamydomonas reinhardtii* (UTEX 90) and *Selenastrum capricornutum* (UTEX 1648). We randomly collected *D. pulicaria* from the clone and let them acclimate to experimental conditions: food (10^5 cells mL⁻¹), light (3.76 TE m⁻² s⁻¹) and temperature (either 8 °C or 20 °C). After 6 hours of acclimation, daphnids were transferred into the filming chamber (190 mL) and we began filming after they resumed normal swimming. We filmed 17 individuals at 20 °C on April 18, 25 and May 11, 1995. On May 8, 10, 1995 we filmed 18 individuals at 8 °C. After filming, individuals were measured from top of head to base of spine. We analyzed swimming tracks as described above and quantified the same swimming variables as described in the multi-factoral seasonal study.

Statistical analysis of laboratory tests for temperature effects

There were no significant differences detected across the days with identical temperatures; therefore, these data were pooled. Data were tested for ANOVA assumptions of normality, skewness and homogeneity of variances (Sokal & Rohlf, 1981). We transformed swimming speed using the reciprocal transformation. We tested for differences between temperatures with ANOVA (F-test) and used a Bonferroni corrected p-value ($0.05/3 = 0.017$) to test for significance.

Laboratory tests for food effects on swimming behavior

To test the effects of food concentrations on swimming behavior, we used *D. pulicaria* Lake Mendota Clone C. The original female of this clone was also collected from Lake Mendota at noon on 3 September 1993 by P. Dawidowicz and raised in our laboratory on *Chlamydomonas reinhardtii* and *Selenastrum* sp.

Algae were maintained in a chemostat culture and grown in Bold's medium. We collected *C. reinhardtii* during the log-growth phase, and counted cell densities with a hemocytometer. We diluted aliquots of *C. reinhardtii* to make the following food concentrations: 0 cells mL⁻¹, 10³ cells mL⁻¹, 10⁴ cells mL⁻¹ and 10⁵ cells mL⁻¹. A concentration of 10⁵ cells mL⁻¹ maximized fitness in *D. magna* (Porter et al., 1983), and at foods levels greater than this, *Daphnia* may eject excess food by sweeping the post abdominal claw, which can interfere with swimming behavior (pers. obs).

Each day of filming, we diluted food concentrations with aged tap water. Twenty adult daphnids, 2.0–2.1 mm, were isolated from the clone and randomly assigned to one of the food levels. We acclimated daphnids to food levels for 1.5–2 h before filming at room temperature (21 °C) and at constant low light levels (3.76 TE m⁻² s⁻¹), and we videotaped five individuals at each food level. Between filming each individual, we agitated the water in the chamber to re-suspend algae. We analyzed and quantified swimming variables as described above. We filmed on January 10, 11, 12 and February 15, 21, 22, 1995. Each day of filming we randomized the order in which food concentrations were filmed.

Statistical analysis of laboratory tests for food effects

We tested data for ANOVA assumptions of normality, skewness (G1, Sokal & Rohlf, 1981), and homogeneity of variances (Levene's test, Milliken & Johnson, 1992). We log-transformed turning angle and swimming speed. However, swimming speed data were not normal even after transformation. Three data points exceeded three standard deviations from the mean; after we removed these outliers and log transformed, data were normally distributed. Data were analyzed with ($n = 116$) and without outliers ($n = 113$). We used ANOVA (F-test) to test for differences among food concentrations using a randomized block design (food level = treatment; day = block) in Systat (1992). The p-value for significance was Bonferroni corrected

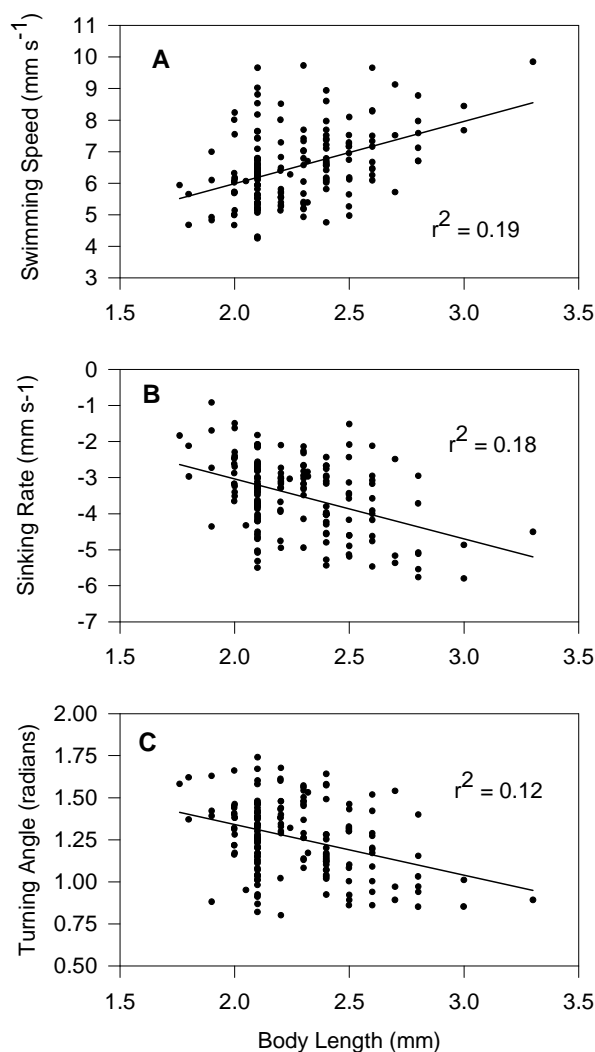


Figure 1. The relationship between *Daphnia* body size (length) and three measurements of swimming behavior. All three correlations are significantly different from zero.

because we tested three variables (Sokal & Rohlf, 1981).

Results

Multi-factor seasonal study of swimming behavior

Sinking rate ($F_{9,179} = 1.377$, $p = 0.242$) and swimming speed ($F_{9,180} = 4.347$, $p = 0.038$, Bonferroni corrected 5% significance level = 0.017) were not significantly different between 2 and 10 m (averages are given in Table 1). We found average turning angle ($F_{9,180} = 9.248$, $p = 0.003$) was significantly

different between depths. Among months, we found significant differences in swimming speed ($F_{9,180} = 15.90$; $p < 0.001$), sinking rate ($F_{9,179} = 25.923$, $p < 0.001$) and turning angle ($F_{9,180} = 22.158$, $p < 0.001$). Multiple regressions were used to determine the influence of temperature and body length on the three response variables: swimming speed, sinking rate and turning angle. Water temperature was not correlated with swimming speed ($F_{1,189} = 3.043$, $p = 0.083$), sinking rate ($F_{1,189} < 0.01$, $p = 0.9$) or turning angle ($F_{1,189} = 0.133$, $p = 0.716$). We found daphnid body length (Figure 1) was significantly correlated with swimming speed ($F_{1,189} = 37.564$, $p < 0.001$, $B_1 = 1.962$), sinking rate ($F_{1,189} = 35.733$, $p = 0.00$, $B_1 = -1.627$) and turning angle ($F_{1,189} = 23.624$, $p < 0.001$, $B_1 = -3.01$). Larger *D. pulicaria* swam and sank faster than small *D. pulicaria*; larger *D. pulicaria* swam in straighter paths than smaller *D. pulicaria*.

We calculated an expected ratio of sinking from Stokes' Law. In this equation (Vogel, 1981) radius and density of the animal cancel, so the relative sinking rate depends on the changes in the coefficients of viscosity at the two temperatures (v_2/v_{24}). At 2 °C viscosity of water is 1.6728 centipoises (cp) and at 24 °C, viscosity of water is .9142 cp (Handbook of Chemistry and Physics 1959); therefore, we predicted sinking rate would be $(1.6728/.9142) = 1.8298$ faster in the 24 °C treatment. We found that sinking rate was -2.71 mm s^{-1} in January, therefore in the warmest months, sinking rate should be $(1.8298 * 2.71) = -4.95 \text{ mm s}^{-1}$. We observed sinking rates to be between -2.95 (June) and -4.08 (July) although the temperature in these months is 24 °C. These observed rates are considerably lower than values predicted by the changes in viscosity.

Temperature effects in the laboratory

For the laboratory study of swimming behavior of a single clone, we found no significant differences were detected in swimming speed ($F_{1,29} = 2.33$; $p = 0.138$), sinking rate ($F_{1,29} = 2.21$; $p = 0.148$) or turning angle ($F_{1,29} = .86$; $p = 0.360$) as a function of water temperature. The ratio of viscosity coefficients at the low and high temperature was calculated to be 1.379 (units cancel: centipoises/centipoises). Therefore, sinking rate at 20 °C should be 1.379 faster than at 8 °C. At 8 °C, the mean sinking rate was -2.46 ; at 20 °C, the mean sinking rate was -2.76 . The observed sinking rate at 20 °C was lower than the

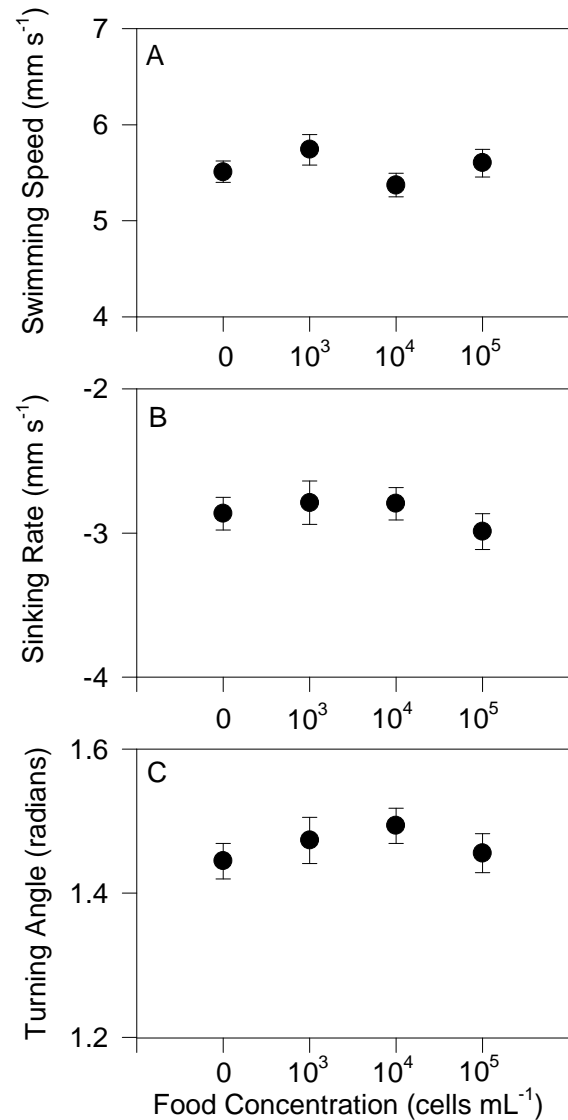


Figure 2. The relationship between food concentration and three measurements of swimming behavior. The error bars are + one standard error of the mean; for none of the behavior variables are the means significantly different.

expected value of $-3.39 (= 1.379 * -2.46)$. A 95% confidence interval around the observed sinking rate of -2.76 ($-2.44, -3.08$) does not include the expected value based on Stokes' Law. Thus, the results imply that sinking rate at 20 °C was slower than expected.

Food effects in the laboratory

There were no significant differences in *D. pulicaria* swimming speed ($F_{3,116} = 1.949$; $p = 0.126$), sinking rate ($F_{3,116} = 1.449$; $p = 0.233$), or turning angle

($F_{3,116} = .461$; $p = 0.710$) as a function of food concentration. When we removed the three outliers, the results were qualitatively the same (i.e. no significant difference). Although power was low (40%) due to the high amount of variance in these data, Figure 2 shows that there is no linear effect of food on any swimming behavior variables.

Discussion

Our results suggest *Daphnia pulicaria* swimming behavior is variable over the annual cycle, but does not change as predicted in response to abiotic and biotic factors. Over the annual cycle, temperature changes dramatically. In agreement with the laboratory results of Gorski & Dodson (1996), we found evidence that *D. pulicaria* modify their behavior so as to sink more slowly at higher temperatures. In the multi-factor seasonal study, we also examined swimming speed in *Daphnia* collected over a range of temperatures. Although swimming speed is a behavior that reflects viscosity and inertial components of a system, swimming speed was lowest in June (low viscosity), and higher in December and January, the two coldest sampling dates with the highest water viscosity.

Neither body length or temperature completely explain the observed changes in sinking rate or swimming speed. *Daphnia* could be changing their effective radius by increasing their carapace gap or changing their body angle to sink in a more horizontal position. Additional mechanisms to alter sinking rate could be changing power output per stroke or area of second antennal spread (Gorski & Dodson, 1996). Biotic factors such as food levels and predation intensity may have a significant impacts on swimming behavior.

In the multi-factor seasonal study, we did not find a significant food effect. Faster swimming was not correlated with clear-water months. In the laboratory experiment, we also found *D. pulicaria* do not swim differently in different food concentrations. These findings agree with Gerritsen and Porter study (1982) for *D. magna*. However, Larsson & Kleiven (1996) found decreased swimming speed in *Daphnia* located in food rich patches. Dodson et al. (1997) compared different clones of *Daphnia* species in the Ploen plankton towers under different food and light levels. He found clones respond differently to similar stimuli. Under high light conditions, *D. pulicaria* swim faster and sink faster in high concentrations of food (unpublished data). The results from different studies suggest that swimming responses to food is dependent on

light regime and the species and clone used. However, investigations have used different scales to address questions about swimming behavior (Brewer, 1996). Our study examined behavior at 1/30 s scale, while other researchers (Larsson & Kleiven, 1996) used a 1 s scale. The use of different scale makes drawing conclusions between foraging and swimming difficult. The results from both our laboratory experiment and seasonal study do not support the hypothesis that *D. pulicaria* swim faster or turn more frequently when food abundance is high. However, Larsson & Kleiven (1996) found that *D. magna* respond to a gradient of food and alter swimming speed when they encounter a food-rich patch. Our study only investigated whether food density affects swimming behavior.

Predation may affect swimming behavior. For example, we found that swimming speed was slow in June and high in July and August (Table 1). During July and August, the Secchi disk depth was low (i.e. very little light penetration) in Lake Mendota; therefore light reaching 2 m is minimal, limiting the possibility of visual predation, and potentially allowing *Daphnia* to swim fast without being seen. A strong clear-water phase occurred in June (Table 1). When the water is clear, it is possible that slow-swimming *Daphnia* are less conspicuous (O'Keefe et al., 1998). In addition, fish predation pressure varies seasonally due to different species hatching and moving into the pelagic zone and/or ontogenic shifts in diets (Post et al., 1992 and Johnson, 1995). Predation by larval cisco (*Coregonus artedii*, a planktivorous whitefish) is greatest in June when they move out into the pelagic zone (Johnson, 1995). Adult fish, white bass (*Morone chrysops*) and yellow perch (*Perca flavescens*) are significant predators on *D. pulicaria* during the months of May and June, 90% of their diets consist of *Daphnia*. During June, predation pressure is intense and Lake Mendota goes through a clear water phase. The interaction between predation and light may favor a slower swimming, making prey less conspicuous. Future studies could explore predation in lakes with greater water clarity and similar predators to discern the importance of light and predation on *Daphnia* swimming ability.

Acknowledgements

We thank the following individuals for support and helpful suggestions during the writing of the manuscript: M. Brewer, P. Gorski, J. Havel, A. Ives,

T. O'Keefe, D. Padilla, J. Shurin, and R. Tollrian. For helpful statistical advice, thanks to D. Faber, A. Ives and D. Padilla. Lisa Lewandowski provided assistance in field sampling and the filming of many zooplankton. A final thank you to P. Dawidowicz for teaching SMR how to film, digitize and analyze swimming tracks.

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