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Individual variability in the swimming behavior of the sub-tropical copepod *Oncaea venusta* (Copepoda: Poecilostomatoida)

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ABSTRACT: The swimming behavior of males and females of the seldom studied sub-tropical copepod *Oncaea venusta* was studied using scale-dependent (swimming speed and net-to-gross displacement ratio) and scale-independent (fractal dimension) metrics. The scale-dependent metrics were characterized by: (1) a considerable intra- and inter-individual variability that prevented the identification of any specific behavior and (2) a strong dependence on the number of data points available in each individual path. Conversely, the scale-independent metric (fractal dimensional) resolved reduced intra- and inter-individual variability and independence from the length of the swimming paths, leading to the identification of 4 groups of distinct swimming patterns. While additional behavioral experiments are needed to ensure the relevance and the generality of the present results, behavioral fractal analysis nevertheless demonstrates a promising ability to elucidate the complexity of zooplankton behavior.

KEY WORDS: Zooplankton · Swimming · Behavior · Scale-dependence · Scale-independence · Fractal · Scaling

INTRODUCTION

In aquatic ecosystems, zooplankton organisms use a range of strategies to search for food, hosts and sexual partners and to avoid predators. Examples encompass a wide spectrum of swimming behaviors, with reported variability related to the species (Tiselius & Jonsson 1990), the age (Coughlin et al. 1992, Van Duren & Videler 1995, Paffenhöfer et al. 1996, Titelman 2001, Titelman & Kiørboe 2003a), food quality and quantity (Tiselius 1992, Bundy et al. 1993, Paffenhöfer & Mazzocchi 2002), the presence of a predator or a conspecific (Van Duren & Videler 1996, Tiselius et al. 1997, Doall et al. 1998, Yen et al. 2004, Titelman & Kiørboe 2003b) or the sex of individuals (Van Duren & Videler 1995, Brewer 1998, Strickler 1998). The information imparted into the surrounding water by a swimming animal (Yen & Strickler 1996, Gries et al. 1999), including both chemical (Weissburg et al. 1998, Yen et al. 1998) and hydromechanical (Costello et al. 1990, Marrasé et al. 1990, Hwang & Strickler 1994, 2001, Hwang et al. 1994, Van Duren et al. 1998, Seuront et al. 2004a) stimuli, has also been reported as a source of behavioral variability.

The movement patterns of zooplankton swimming behavior are also likely to be affected by environmental complexity such as resource patchiness (Tiselius 1992, Tiselius et al. 1993). Considering the increasing awareness of the heterogeneous nature of physical and biological patterns and processes at scales relevant to individual organisms (Cowles et al. 1998, Seuront et al.

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1996a,b, 1999, 2002, Seymour et al. 2000, 2004, Waters & Mitchell 2002, Waters et al. 2003, Seuront & Schmitt 2004), there is a genuine need to establish a reference framework that will link pure behavioral observations, the qualitative and quantitative nature of environment complexity and zooplankton trophodynamic hypotheses (Keiyu et al. 1994, Seuront et al. 2001, 2004b, Schmitt & Seuront 2001, 2002). Key processes such as competition, mating and predation occur across distances of centimeters; however, the consequences of these interactions influence processes such as climate and fisheries productivity up to the global scale (Kolber et al. 2001, Rivkin & Legendre 2001). In this context, and considering the extremely intertwined properties of swimming and feeding processes in copepod ecology (Jiang 2004), the testing of mechanistic hypotheses relating individual movements to higher-level ecological phenomena requires that individual swimming pathways be precisely characterized, both qualitatively and quantitatively.

This task may be more challenging than it appears at first glance. In addition to the widely acknowledged difficulty associated with collecting time series of 3-dimensional high-spatial-resolution behavioral data, previous behavioral studies were subject to legitimate criticism related to the few replicates of individual animals examined and/or to the tethering techniques used to maintain the animal in focus. Turner et al. (1993) thus reported that in terms of time allocation to various behaviors, animal-to-animal variability of 5 tethered adult females of *Calanus finmarchicus* was significantly greater than any pattern related to food concentration. Hwang et al. (1993) found that for a group of 10 adult females of *Centropages hamatus*, variability for tethered animals was significantly greater than for free-swimming ones. As individual variability has also been highlighted in copepod feeding activity (Paffenhöfer 1994, Paffenhöfer et al. 1996), we stress the need to assess the behavioral ecology of copepods by investigating numerous free-swimming animals.

In addition, behavioral ecologists face another, more fundamental, problem (Seuront et al. 2004b). Most of the quantitative metrics commonly applied in behavioral studies, e.g. path length, turning rate and net-to-gross displacement ratio (NGDR), are indeed scale dependent. That is, the metrics will take on different values depending on the physical or temporal scale at which they are measured (Seuront et al. 2004b). This issue is even more critical considering that individual studies typically recorded behaviors at different temporal resolutions, i.e. ranging from 0.01 to 60 Hz (Table 1). The scale dependence inherent in most metrics results in there being no single scale at which swimming paths can be unambiguously described. Thus, there is no single scale at which swimming behaviors can be compared without leading to arbitrary and potentially spurious conclusions. Despite the limitations related to scale-dependent metrics, as far as we know, only a few studies have analyzed plankton swimming behavior in a scale-independent framework (Table 1).

Considering that only few zooplankton species (mainly calanoids in the marine environment, see Table 1) have been the subject of behavioral studies, the objective of this work is to extend behavioral studies to the seldom-studied sub-tropical copepod *Oncaea venusta*. *O. venusta* is a very common and widely distributed copepod species in the waters of Taiwan (Hwang & Turner 1995, Shih & Chiu 1998, Lo et al. 2001, 2004, 2004, Hsieh & Chiu 2002, Wu et al. 2004), Japan (Ueda 1991) and Hong Kong (Chen et al. 2003, Lee & Chen 2003). A preliminary study of swimming behavior of *O. venusta* females under a dissecting microscope was carried out by Hwang & Turner (1995). In the past decade, a laser video optical system has been commonly used to observe the swimming trajectories and behavior of tiny marine organisms (Costello et al. 1990, Marrasé et al. 1990, Trager et al. 1990, Hwang et al. 1993, 1994, 1998, Hwang & Strickler 1994, 2001, Strickler & Hwang 1999, Shih & Hwang 2000). We used a similar technique for this study. On the basis of an extended data set including 44 swimming paths we investigated: (1) the scale-independent properties of the swimming behavior of *O. venusta* and (2) the individual variability in the swimming behavior of free-swimming males. Standard scale-dependent metrics such as swimming speed and NGDR have been estimated as a reference framework and compared to the scale-independent analysis. Finally, the implications of the observed patterns are discussed in the general framework of the behavioral ecology of zooplankton.

MATERIALS AND METHODS

Experimental procedures and behavioral observations. Copepods were collected in surface, free-drifting net tows with standard Norpac zooplankton nets (45 cm mouth diameter, 180 cm in length and 333 µm mesh) from offshore waters near the National Taiwan Ocean University, Keelung, on the northeast coast of Taiwan. All sampling was conducted by 'Ocean Research Vessel II' in the daytime from 18 to 22 July 1997. There were several cruises per day to collect actively swimming copepods. Samples were returned to the laboratory within <1 h of each cruise, and actively swimming adult copepods of *Oncaea venusta* were sorted into rectangular experimental vessels of 5 × 10 × 10 cm containing 400 ml of 63 µm screened natural seawater from the site of collection. To avoid confounding the swimming behavior of males and

Table 1. Literature survey of zooplankton behavioral studies, arranged in chronological order from 1964 to 2004 (1NGDR: net-to-gross displacement rate; 2MFDR: length of male pursuit trajectory/length of female trajectory; 3RMSD: root-mean-sqaure displacement)

Organism	View	Variable	Metrics [temporal scale]	Authors
Daphnia[b]	2D, side	Relative light intensity	Speed, position in the water column [–]	Ringelberg (1964)
Cyclops[b]	2D, side	Light	Speed [0.1 Hz]	Strickler (1970)
Daphnia[b]	2D, top	Polarized light	Speed, NGDR, IDT, turning rate [30 Hz]	Wilson & Greaves (1979)
Mesocyclops[b]	2D, top	Prey patches	Speed, loops/min [0.01 Hz]	Williamson (1981)
Daphnia[b]	3D	Angular light distribution	Speed, NGDR1 [–]	Buchanan et al. (1982)
Daphnia[b]	2D, side	Food concentration	Speed [0.1 Hz]	Porter et al. (1982)
Acartia	2D, top	Bioluminescent dinoflagellates	Speed, NGDR1, bursts [15 Hz]	Buskey et al. (1983)
Pseudocalanus	2D, top	Food concentration and odors	Speed, NGDR1, bursts, pauses [15 Hz]	Buskey (1984)
Diaptomus	2D, top	Predators & competitors	Speed, NGDR1, time between jumps [30 Hz]	Wong et al. (1986)
Daphnia[b]	3D	Food concentration	Speed, turning rate, ground covered [30 Hz]	Young & Getty (1987)
Euchaeta	3D	Predator–prey/male–female interactions	Speed, turning rate	Yen (1988)
Favella	2D, side	Food patches	Speed, NGDR1, turning rate [15 Hz]	Buskey & Stoecker (1988)
Thysanoessa	3D	Algal patches	Speed, NGDR1, bursts, %sinking [2 Hz]	Price (1989)
Six calanoids	2D, side	Light, food type	Speed, foraging mode [12.5 Hz]	Tiselius & Jonsson (1990)
Polyphemu	2D, top	Predator–prey interaction	Speed, turning rate, meander [1 Hz]	Young & Taylor (1990)
Bosmina	2D, top	Predator–prey interaction	Speed, turning rate, meander [1 Hz]	Young & Taylor (1990)
Daphnia	3D	Body size	Speed, displacement angle, NGDR, stroke velocity, sinking speed [30 Hz]	Dodson & Ramcharan (1991)
Diaptomus	3D	Predators	Speed, jump length, angle of motion [20 Hz]	Ramcharan & Sprules (1991)
Diaptomus	2D, top	Conspecifics	Speed, NGDR1 [–]	Van Leeuwen & Maly (1991)
Acartia	2D, side	Turbulence	Speed, foraging activity and behavior [25 Hz]	Saiz & Alcaraz (1992)
Amphiprion[a]	3D	Food concentration	Speed, NGDR1, turning angles, fractal dimension [10–15 Hz]	Coughlin et al. (1992)
Acartia	2D, side	Food patches	Speed, vertical position, jump frequency, NGDR [0.1 Hz]	Tiselius (1992)
Centropages	3D	Food concentration	Speed, NGDR1, Realized Encounter Volume, i.e. fractal dimension [30 Hz]	Bundy et al. (1993)
Various species	2D, side	Species	Speed, NGDR1, rate of change in direction [15–30 Hz]	Buskey et al. (1993)
Diaptomus	2D, top	Gravid females	Speed, NGDR1 [–]	Maly et al. (1994)
Acartia	3D	Food, turbulence	Speed, behavioral observations [30 Hz]	Saiz (1994)
Oithona	2D, top	Behavior	Duration of swimming/non–swimming behaviors, behavioral transitions frequency [3 Hz]	Hwang & Turner (1995)
Temora	2D, top	Behavior	Duration of swimming/non–swimming behaviors, behavioral transitions frequency [3 Hz]	Hwang & Turner (1995)
Macrosetella	2D, top	Behavior	Duration of swimming/non–swimming behaviors, behavioral transitions frequency [3 Hz]	Hwang & Turner (1995)
Undinula	2D, top	Behavior	Duration of swimming/non–swimming behaviors, behavioral transitions frequency [3 Hz]	Hwang & Turner (1995)
Oncaea	2D, top	Behavior	Duration of swimming/non–swimming behaviors, behavioral transitions frequency [3 Hz]	Hwang & Turner (1995)
Brachionus	2D, top	Toxic stress	Speed, sinuosity, behavioral observations [25 Hz]	Charoy et al. (1995)
Temora	3D	Food concentration	Speed, NGDR1, behavioral observations [50 Hz]	Van Duren & Videler (1995)
Dioithona	2D, side	Light, water flow	Speed, rate of change in directions [30 Hz]	Buskey et al. (1996)
Oithona	2D	Developmental stage	Speed, behavioral observations [30 Hz]	Paffenhöfer et al. (1996)
Temora	2D, 3D	Predators, conspecifics	Speed, NGDR1, behavioral observations [50 Hz]	Van Duren & Videler (1996)
Daphnia[b]	3D	Food concentration, light, temperature	Speed, turning angle, turning rate, NGDR, fractal dimension [10 Hz]	Brewer (1996)
Daphnia[b]	2D, top	Food concentration	Speed [–]	Larsson & Kleiven (1996)
Daphnia[b]	3D	Light, food concentration, vessel size	Speed, turning angle [30 Hz]	Dodson et al. (1997)
Acartia	2D	Predators	Encounter rates [–]	Tiselius et al. (1997)
Euplotes	2D, top	Food patches	Speed, motility, fractal dimension [–]	Jonsson & Johansson (1997)
Protoperidinium	2D, top	Food type	Speed, rate of change of direction, behavioral observations [15 Hz]	Buskey (1997)
Centropages	2D	Turbulence, food concentration	%Swimming, swimming behavior, jumps [25 Hz]	Caparroy et al. (1998)

Table 1. (continued)

Organism	View	Variable	Metrics [temporal scale]	Authors
Cyclops[b]	3D	Conspecifics	Speed, distance between male and female [60 Hz]	Strickler (1998)
Daphnia[b]	3D	Predators	Speed, turning angle, behavioral observations [30 Hz]	O'Keefe et al. (1998)
Temora	3D	Sex, mating	Speed, NGDR1, encounter, MFDR2 [60 Hz]	Doall et al. (1998)
Temora	3D	Sex, mating	Speed, turning angle, NGDR1 [60 Hz]	Weissburg et al. (1998)
Calanus	2D	Sex, mating	Speed, behavioral observations [0.27–4.55 Hz]	Tsuda & Miller (1998)
Temora	3D	Sex, mating	Speed, RMSD3, diffusion	Yen et al. (1998)
Daphnia	3D	Sex, mating	Speed, turning angle, distance between male and female [25 Hz]	Brewer (1998)
Lates calcarifer[a]	2D, top	Food concentration	Pause duration, distance travelled between pauses, travel duration, developmental stage, fractal dimension [25 Hz]	Dowling et al. (2000)
Pomacentrus[a]	1D, side	Age	Speed [–]	Fisher et al. (2000)
Sphaeramia[a]	1D, side	Age	Speed [–]	Fisher et al. (2000)
Amphiprion[a]	1D, side	Age	Speed [–]	Fisher et al. (2000)
Acartia	2D, side	Predators	Speed, reaction distance, jumps [60 Hz]	Suchman (2000)
Acartia	3D	Age, predators	Speed, jump directionality, frequency, length and speed [–]	Titelman (2001)
Temora	3D	Age, predators	Speed, jump directionality, frequency, length and speed [–]	Titelman (2001)
Temora	3D	Behavior	Multifractal parameters [12.5 Hz]	Schmitt & Seuront (2001, 2002)
Oithona	3D	Food quality and quantity	Sinking speed and modality, frequency, speed and direction of jumping [60 Hz]	Paffenhöfer & Mazzocchi (2002)
Clupea harengus[a]	2D	Age, turbulence, light	Attack rate and swimming activity (duration of time swimming and duration of swimming bout) [–]	Utne-Palm & Stiansen (2002)
Euchaeta	3D	Prey	Speed, attack volume and angle [60 Hz]	Doall et al. (2003)
Oxyrrhus marina	2D	Food quantity	Lévy distribution, i.e. fractal dimension [12 Hz]	Bartumeus et al. (2003)
Goldfish[a]	2D	Behavior	Lévy distribution, i.e. fractal dimension [30 Hz]	Faure et al. (2003)
Acartia	3D	Age	Sinking, swimming and jumping speed, behavioral observations [25 Hz]	Titelman & Kiørboe (2003a)
Calanus	3D	Age	Sinking, swimming and jumping speed, behavioral observations [25 Hz]	Titelman & Kiørboe (2003a)
Centropages	3D	Age	Sinking, swimming and jumping speed, behavioral observations [25 Hz]	Titelman & Kiørboe (2003a)
Euterpina	3D	Age	Sinking, swimming and jumping speed, behavioral observations [25 Hz]	Titelman & Kiørboe (2003a)
Temora	3D	Age	Sinking, swimming and jumping speed, behavioral observations [25 Hz]	Titelman & Kiørboe (2003a)
Acartia	3D	Age, predators	Sinking and swimming speed, escape jump length, speed and direction [25 Hz]	Titelman & Kiørboe (2003b)
Calanus	3D	Age, predators	Sinking and swimming speed, escape jump length, speed and direction [25 Hz]	Titelman & Kiørboe (2003b)
Centropages	3D	Age, predators	Sinking and swimming speed, escape jump length, speed and direction [25 Hz]	Titelman & Kiørboe (2003b)
Euterpina	3D	Age, predators	Sinking and swimming speed, escape jump length, speed and direction [25 Hz]	Titelman & Kiørboe (2003b)
Temora	3D	Age, predators	Sinking and swimming speed, escape jump length, speed and direction [25 Hz]	Titelman & Kiørboe (2003b)
Daphnia	2D, side	Turbulence, light	Speed, direction of motion, fractal dimension [30 Hz]	Seuront et al. (2004a)
Temora	2D, side	Turbulence, light	Speed, direction of motion [30 Hz]	Seuront et al. (2004a)
Daphnia[b]	3D	Behavior	Path length, turning angle, fractal dimension [12.5 Hz]	Seuront et al. (2004b)
Daphnia[b]	3D	Behavior	Multifractal parameters [12.5 Hz]	Seuront et al. (2004c)
Temora	3D	Behavior	Multifractal parameters [12.5 Hz]	Seuront et al. (2004c)

[a]Fish
[b]Freshwater species

females due to the presence of the opposite sex, separate experiments were conducted on males (size range: 0.90 to 1.00 mm) and females (0.80 to 1.16 mm). The similar laser video optical systems of Hwang et al. (1994), Hwang & Strickler (1994, 2001), Strickler & Hwang (1999) were used in this study to examine the swimming behavior of *O. venusta*. The experiment was done by filming actively free-swimming *O. venusta*, using a laser light source with a video camera, a videocassette recorder, a frame counter and a monitor.

Quantifying zooplankton swimming behavior. Movement paths may be characterized by a variety of measures (Table 1), including path length (the total distance traveled, or gross displacement), move length (the distance traveled between consecutive points in time), move duration (the time interval between successive pauses, as well as between successive spatial points), speed (the move length divided by move duration), turning angle (the difference in direction between 2 successive moves), turning rate (the turning angle divided by move duration), net displacement (the linear distance between starting and ending point, i.e. NGDR), and fractal dimension. For paths recorded at fixed time intervals, move duration is a constant. As extensively discussed in Seuront et al. (2004b), the values of all the metrics are implicitly a function of their measurement scale (Fig. 1). The scale dependence of standard metrics implies that there is no single scale at which swimming paths can be unambiguously described. This is not the case, however, for fractal dimensions, which are independent of scale and therefore have the potential to become a reference framework in analyzing and inferring behavioral data. Because fractal dimensions have seldom been applied to zooplankton behavior (Table 1), we also used 2 of the most common behavioral measures, swimming speed and NGDR, as a reference framework to allow the reader to make comparisons with previous studies having similar temporal resolution.

Swimming speed and NGDR: The distance d (mm) traveled between 2 successive video frames was computed from the (x, y) coordinates as:

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

where (x_t, y_t) and (x_{t+1}, y_{t+1}) are the positions of a copepod at time t and t + 1, respectively. The swimming speed v (mm s^{-1}) was subsequently estimated as:

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

where f is the sampling rate of the camera, i.e. f = 30 frame s^{-1}. Average swimming speeds and their standard deviations were measured over the duration of each individual track.

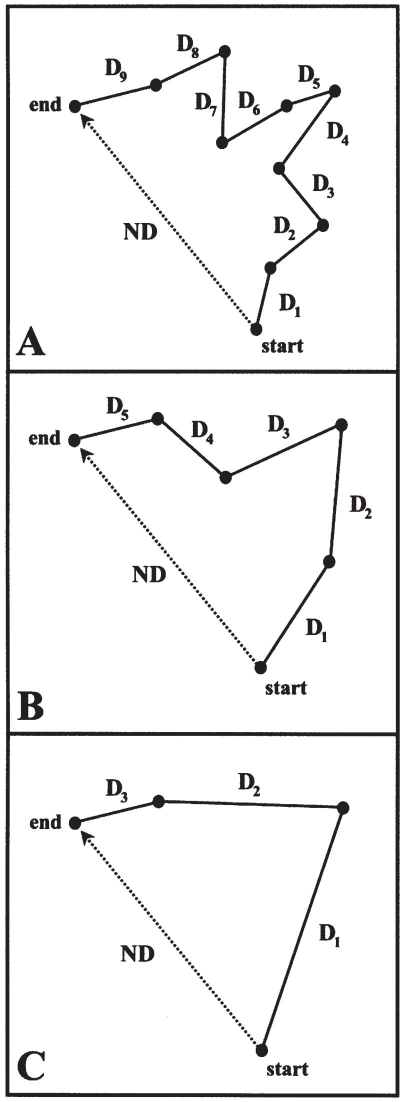

Fig. 1. Illustration of the concept of scale dependence in the net-to-gross displacement rate (NGDR) shown at 3 different resolutions. The net displacement (ND) is the straight-line distance between the initial and final locations, and the growth displacement is the sum of the distances D_i

NGDRs were computed according to Buskey (1984):

$$\text{NGDR} = \text{ND/GD} \qquad (3)$$

where ND (mm) and GD (mm) are the net and gross displacements of a copepod, which correspond to the shortest distance between the starting and ending points of the trajectory and the actual distance traveled by the copepod, respectively. The NGDR provides a measure of the relative linearity of copepod swimming paths, with lower NGDRs implying more curved trajectories than higher NGDRs. NGDRs were computed at the smallest available resolution (i.e. $\frac{1}{30}$ s) for each individual track.

Fractal dimension: The above-stated traditional metrics used to characterize animal movements are scale dependent; see Seuront et al. (2004b) for further discussion. We thus used fractal analysis, which is based on the premise that the fractal dimension can serve as a scale-independent descriptor of the path an organism takes as it swims about. If an organism moves along a completely linear path, then the actual distance traveled, L, equals the displacement between the start and the finish, l. The relationship between these 2 variables is linear. In other words, if we assume a power law relating L to l, i.e. $L^D = l$, then the exponent $D = 1$. According to this power law, if the path deviates from linearity, that is, becomes curvy, the exponent will then be > 1. In the extreme example of curviness, i.e. for the case of Brownian motion in 2 dimensions, $D = 2$ (Mandelbrot 1983). It appears that D provides a measure of the path 'complexity', with the extreme cases delineated by linear and Brownian movement, respectively. Real-life cases are expected to fall between these extremes.

Formally, the fractal dimension D is estimated by superimposing a regular grid of pixels of length λ on the object and counting the number of 'occupied' pixels (Fig. 2). This procedure is repeated using different values for λ. The volume occupied by a path is then estimated with a series of counting boxes, spanning a range of volumes down to some small fraction of the entire volume (Fig. 2). The number of occupied boxes increases with decreasing box size, leading to the following power-law relationship:

$$N(\lambda) = k_1\lambda^{-D} \tag{4}$$

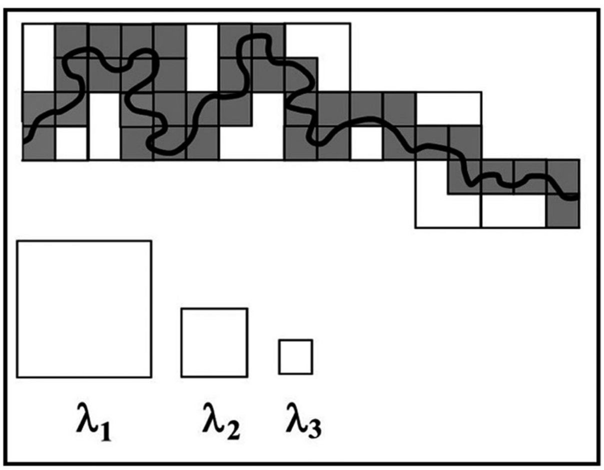

Fig. 2. Two-dimensional illustration of the box-counting method used to describe swimming path complexity with fractal dimension. Three steps of the analyses are shown, using 3 different characteristic box sizes λ_1, λ_2 and λ_3

where λ is the box size, $N(\lambda)$ is the number of boxes occupied by the path, k is a constant and D is the box-counting fractal dimension, also referred to as the box dimension. D is estimated from the slope of the linear trend of the log–log plot of $N(\lambda)$ versus λ. Because slight reorientation of the overlying grid can produce different values of $N(\lambda)$ (Appleby 1996), the fractal dimension D has been estimated for rotation of the initial 2D grid of 5° increments from 0 to 45°.

Because an objective procedure is needed to decide upon an appropriate range of scales to include in the regressions, we used the values of the time scales, which satisfied a statistically sound criterion. We consider a regression window of varying width ranging from a minimum of 5 data points (the least number of data points to ensure the statistical relevance of a regression analysis) to the entire data set. The smallest windows are slid along the entire data set at the smallest available increments, with the whole procedure iterated $n - 4$ times, where n is the total number of available data points. Within each window and for each width, we estimated the coefficient of determination (r^2) and the sum of the squared residuals for the regression. We subsequently used the values of λ (Eq. 4), which maximized the coefficient of determination and minimized the total sum of the squared residuals (Seuront & Lagadeuc 1997, Seuront et al. 2004b,c), to define the scaling range and to estimate the related dimensions D.

Statistical analyses. As the distribution of the estimated parameters (swimming speed, NGDR and fractal dimension) were non-normally distributed (Kolmogorov–Smirnov test, $p < 0.01$), non-parametric statistics were used throughout this work. Male–female comparisons were carried out using the Wilcoxon Mann-Whitney U-test (WMW test hereafter). Multiple comparisons between males and females were conducted using the Kruskal-Wallis test (KW test hereafter), and the Jonckheere test for ordered alternatives (Siegel & Castellan 1988) was used to identify distinct groups of fractal dimensions.

The intra-individual and inter-individual variability was expressed as the coefficient of variation CV ($CV = SD/\bar{x}$) of swimming speeds and fractal dimensions estimated within and between all individual paths. Because 1 NGDR value was obtained for each individual path, only the inter-individual variability in NGRDs was considered.

Correlation between variables was investigated using Kendall's coefficient of rank correlation, τ (Kendall & Stuart 1966). Kendall's coefficient was used in preference to Spearman's coefficient of correlation ρ — although recommended in Kendall (1976) — because Spearman's ρ gives greater weight to pairs of ranks that are further apart, while Kendall's τ weights each

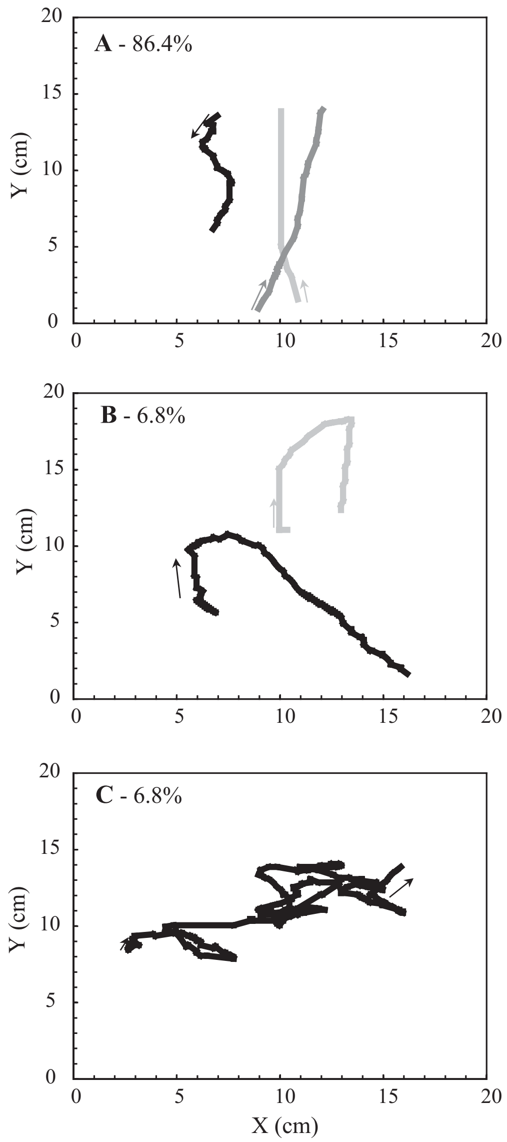

Fig. 3. *Oncaea venusta*. The 3 types of swimming behavior observed for males and referred to as rectilinear (A), 'A-shaped' (B) and tortuous (C)

disagreement in rank equally; see Sokal & Rohlf (1995) for further discussion.

RESULTS

Swimming paths

Four types of swimming paths were visually identified for males and females of *Oncaea venusta*: rectilinear, 'A-shaped', 'V-shaped' and convoluted (Figs. 3 & 4). A rectilinear swimming path (Figs. 3A, 4A) was the dominant swimming behavior observed for males (86.4%) and females (76.7%). These paths were traveled mainly in a vertical direction, for both males and females. 'A-shaped' and 'V-shaped' swimming paths were observed specifically for males (6.8%) and females (13.7%). Male 'A-shaped' paths were always traveled upward and downward (Fig. 3B), while female 'V-shaped' paths were traveled downward and upward (Fig. 4B). Finally, males and females showed tortuous swimming paths (6.8% of males and 9.6% of females) that were restricted to the vertical direction for females (Fig. 4C) and more isotropic for males (Fig. 3C).

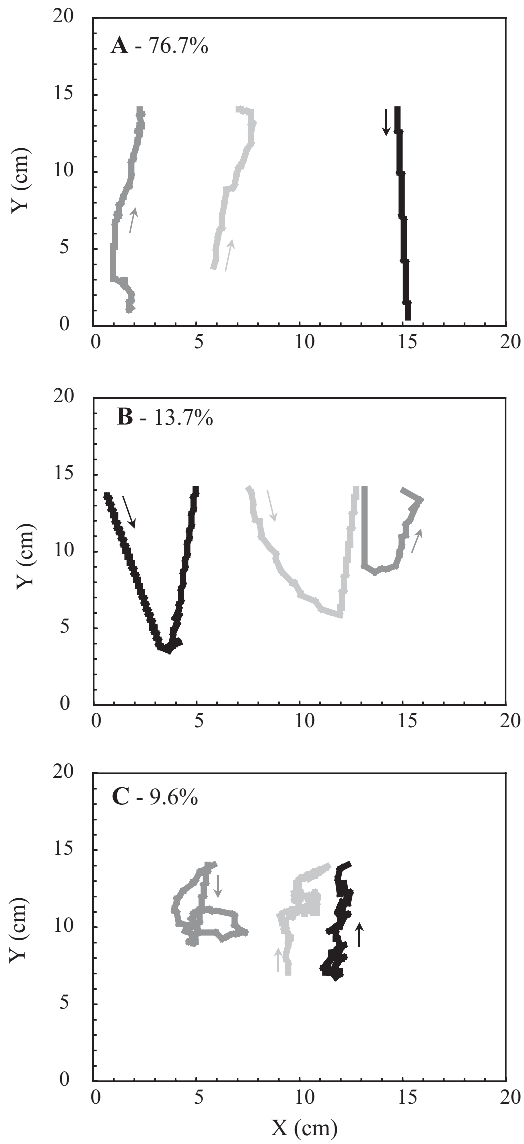

Fig. 4. *Oncaea venusta*. The 3 different types of swimming behaviors observed for females, and referred to as rectilinear (A), 'V-shaped' (B) and tortuous (C)

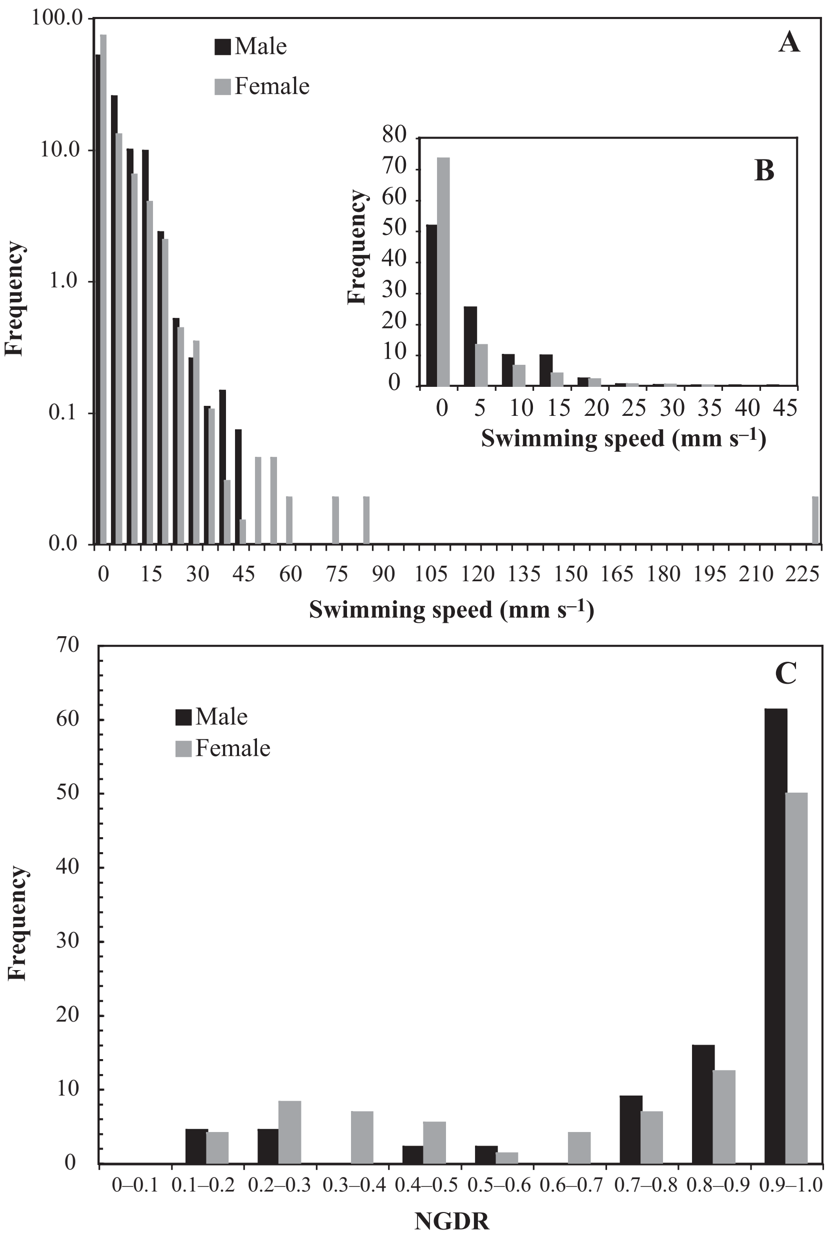

Fig. 5. *Oncaea venusta*. Swimming behavior of males (n = 44) and females (n = 73). (A) Frequency distribution of individual swimming speed measurements (n = 2728 for males and n = 6641 for females; logarithmic *y*-axis coordinates for speed ranging from 0 to 235 mm s^{-1}). (B) Frequency distribution of individual swimming speed measurements for speed ranging from 0 to 50 mm s^{-1}. (C) Frequency distribution of net-to-gross displacement ratios (NGDR) computed from 2728 and 6641 individual spatial positions for males and females, respectively

Swimming speed and NGDR

The swimming speeds of males and females of *Oncaea venusta* ranged from 0 to 46.6 mm s^{-1} and 0 to 231.3 mm s^{-1}, respectively. While the frequency distribution of females is significantly more skewed than that of males (Figs. 5A, 6A & B), males and females traveled at statistically similar speeds (WMW test, $p > 0.05$), averaging, respectively, 9.44 ± 4.86 mm s^{-1} and 7.99 ± 5.41 mm s^{-1} ($\bar{x}$ ± SD). However, significant differences (χ^2 test, $p < 0.01$) were found between the frequency of individual swimming speed measurements bounded between 0 and 5 mm s^{-1} and between 5 and 20 mm s^{-1}. A significantly higher proportion of swimming speed < 5 mm s^{-1} was observed for females (Figs. 5A & B, 6A), while a higher proportion of swimming speed bounded between 5 and 20 mm s^{-1} was found for males (Figs. 5A & B, 6B).

The NGDRs of males ranged from 0.11 to 1.00, averaging 0.84 ± 0.24 ($\bar{x}$ ± SD; Figs. 5C, 6C). The NGDRs of females were not significantly different (Figs. 5C, 6D; WMW test, $p > 0.05$), ranging from 0.14 to 1.00 and averaging 0.76 ± 0.28 ($\bar{x}$ ± SD; reflecting similar curves and loops in male and female swimming trajectories. A significantly higher proportion of NGDRs were nevertheless found in the range from 0.9 to 1.0 (Fig. 5C, χ^2 test, $p < 0.01$), suggesting that the swimming behavior of males and females of *Oncaea venusta* was essentially rectilinear.

The observation of swimming speed and NGDR as the function of individual paths (Fig. 6) showed a predominance of individual variability. The intra-individual variability of swimming speed thus ranged from 0.06 to 1.41 for males and from 0.01 to 2.14 for females. The intra-individual variability is significantly higher for females than for males (WMW test, $p > 0.05$). The inter-individual variability of swimming speed is also higher for females (CV = 0.64) than for males (CV = 0.39), as the NGDR inter-individual variability was CV = 0.28 for males and CV = 0.39 for females. Finally, no correlations were found between the 4 types of swimming paths and swimming speeds described above. NGDRs were consistently higher for tortuous and 'A-shaped' swimming paths for males (Fig. 6C), while for females low NGDRs (Fig. 6D) also included some rectilinear swimming paths (see Fig. 3A).

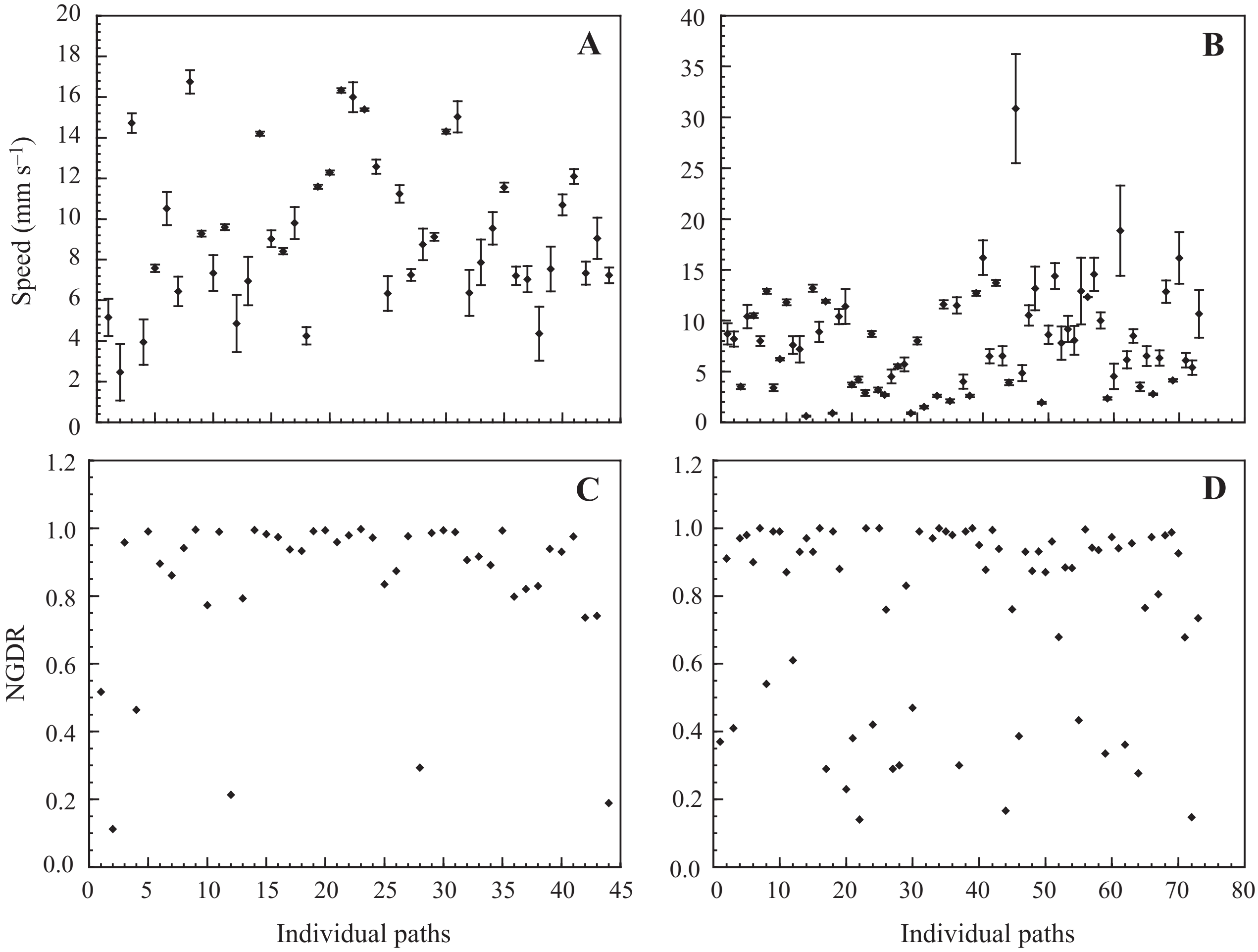

Fig. 6. *Oncaea venusta*. Swimming speeds and net-to-gross displacement ratios (NGDR) as a function of individual paths for males (A, C) and females (B, D). Error bars are SD

Fractal dimension

Log–log plots of $N(\lambda)$ versus λ exhibited a very strong linear behavior for males (Fig. 7A) and females (Fig. 7B) over the whole range of available scales (i.e. from 1 to 200 mm) with coefficient of determination r^2 ranging from 0.98 to 0.99. A clear scaling behavior was observed from 1 to 200 mm for the 44 individual male paths and 66 of the female paths. In addition, 6 of the female paths showed 2 distinct scaling behaviors at scales smaller and larger than 10 mm (Fig. 8). This third group is hereafter referred to as G_{10}. The shortest female path (No. 32) did not exhibit any scaling behavior because of the small number of data points (i.e. n = 19). The resulting fractal dimensions, plotted as a function of individual paths (Fig. 9), showed a lower inter-individual variability for males (Fig. 9A) than for females (Fig. 9B). Nevertheless the male and female fractal dimensions (D_m and D_f), averaging D_m = 1.14 ± 0.06 (mean ± SD) and D_f = 1.15 ±

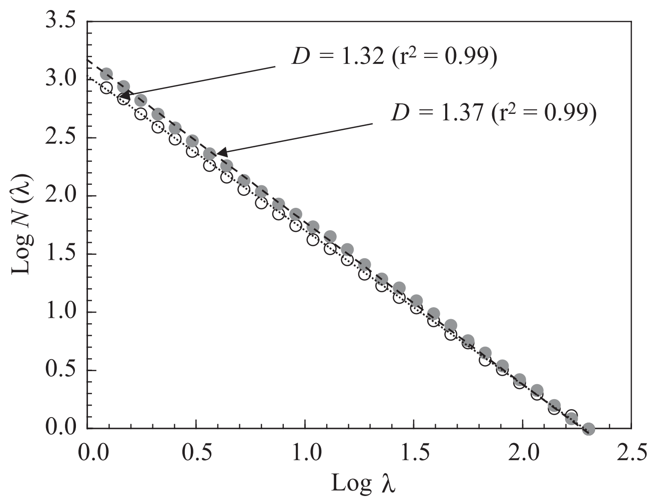

Fig. 7. *Oncaea venusta*. Illustration of the scaling behavior of the log–log plots of $N(\lambda)$ versus λ for the individual male Path 44 (closed symbols) and the female Path 59 (open symbols)

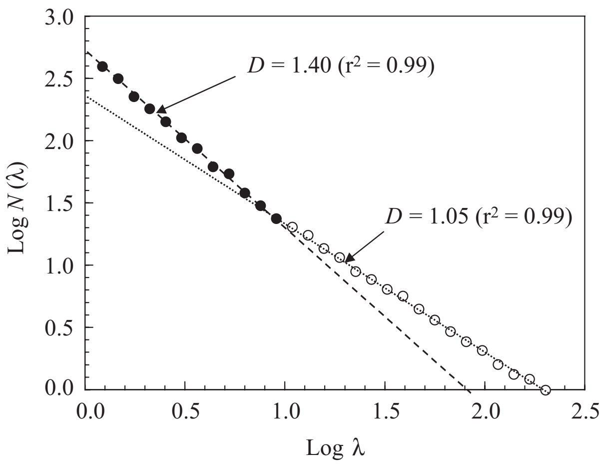

Fig. 8. *Oncaea venusta*. Illustration of the 2 distinct scaling behaviors of the log–log plots of $N(\lambda)$ versus λ for the individual female Path 42

0.06, cannot be statistically distinguished (WMW test, $p > 0.05$). The fractal dimensions of the 2 types of path for the G_{10} group $D_{>10} = 1.35 \pm 0.05$ (mean ± SD) and $D_{<10} = 1.02 \pm 0.01$ were significantly different from each other (WMW test, $p < 0.01$). These 2 groups of fractal dimensions ($D_{>10}$ and $D_{<10}$) corresponded to Paths 8, 42, 66–68 and 70. As observed for swimming speeds and NGDRs, the distributions of the fractal dimensions among individual paths were characterized by an elevated individual variability (Fig. 9). CV in the individual fractal dimensions ranged from 0.01 to 0.19 for males and from 0.00 to 0.16 for females. CV between individual fractal dimensions was 0.056 for males and 0.049 for females.

As the fractal dimensions were significantly different within males and females (KW test, $p < 0.01$), the origin of the observed variability in fractal dimensions was more thoroughly investigated using the Jonckheere test for ordered alternatives (Siegel & Castellan 1988) to identify distinct groups of fractal dimensions. Four groups of significantly different fractal dimensions D_m were identified for the male paths (Fig. 9A). These groups were classified by decreasing fractal dimension values as: G_{m1} (Paths 12, 27, 35), G_{m2} (Paths 1, 2, 4), G_{m3} (Paths 3, 6–8, 13–26, 28–34, 36–44) and G_{m4} (Paths 5, 9, 11). Three groups were identified for female paths (Fig. 9B) and classified by decreasing fractal dimension values as G_{f1} (Paths 1, 3, 17, 20, 28, 59), G_{f2} (Paths 2, 4–7, 9–12, 13–16, 18–19, 21–27, 29–31, 34–41, 43–58, 60–65, 69, 71–73) and G_{f3} (Path 33). The fractal dimensions of groups G_{f1} and G_{f2} were, respectively, significantly smaller and higher than the fractal dimensions of groups $G_{>10}$ and $G_{<10}$ (Jonckheere test, $p < 0.05$). The fractal dimensions of groups G_{f3} and $G_{<10}$ were not significantly different (Jonckheere test, $p < 0.05$).

Correlation analyses

Correlation analyses were done between the number of data points in each individual swimming trajectory, swimming speed, NGDR and fractal dimensions for males and females (1) to infer the potential effect of the length of an individual swimming path on the estimates of behavioral metrics and (2) to investigate the relationships between these metrics for males and females. The analyses showed that swimming speed and NGDR were significantly negatively correlated with the length of the trajectories for males and females, while fractal dimensions were not (Table 2). Swimming speed and NGDR were significantly positively correlated, and fractal dimensions and NGDR were significantly negatively correlated (Table 2).

DISCUSSION

Robustness of fractal dimension estimates

Fielding (1992), Hastings & Sugihara (1993), Kenkel & Walker (1993) and Seuront et al. (2004b) previously suggested that to ensure the meaning and the reliability of fractal dimension estimates, different methods should be used on the same data sets. Here, we used a method conceptually similar to the box-counting procedure, i.e. the compass procedure. Using this procedure, the fractal dimension is estimated by measuring the length L of a path at various scale values δ. This approach was initially introduced by Richardson (1961) to measure the length of the coast of Brittany. He showed that this length is not defined as an absolute value, but has a length varying with the resolution used for the measurements. This was later conceptualized as a frac-

Table 2. *Oncaea venusta*. Correlation matrix of variables relative to the behavior of males and females of the copepod (time: duration of the swimming paths of *O. venusta* analyzed; v: mean swimming speed; NGDR net-to-gross displacement rate; D: fractal dimension). *5% significance level; **1% significance level

	Time	v	NGDR	D
Males				
Time	–	–	–	–
v	−0.532**	–	–	–
NGDR	−0.323*	0.474**	–	–
D	0.201	−0.264	−0.364*	–
Females				
Time	–	–	–	–
v	−0.704**	–	–	–
NGDR	−0.400*	0.280*	–	–
D	0.182	−0.174	−0.608*	–

tal dimension for movement pathways by Mandelbrot (1983), and it is also called the 'latent dimension' by Feder (1988). The procedure is analogous to moving a set of dividers (like a drawing compass) of fixed length δ along the path. The estimated length of the path is the product of N (number of compass dividers required to 'cover' the object) and the scale factor δ. The number of dividers necessary to cover the object then increases with decreasing measurement scale, giving rise to the power-law relationship:

$$L(\delta) = k_2\delta^m \quad (5)$$

where δ is the measurement scale, $L(\delta)$ is the measured length of the path, $L(\delta) = N\delta$, and k_1 is a constant. Practically, the fractal dimension D_c is estimated from the slope m of the log–log plot of $L(\delta)$ versus δ for various values of δ where:

$$D_c = 1 - m \quad (6)$$

Hereafter, the fractal dimension D_c will be referred as the 'compass dimension'. As the values $L(\delta) = N\delta$ may vary depending on the starting position along the curve (Seuront et al. 2004b), we obtained a distribution of the compass dimensions by repeatedly starting the compass procedure at different, randomly chosen, positions. The resulting compass dimensions D_c', estimated from 10 random starting positions for each of the 127 swimming paths available, do not show significant differences ($p > 0.05$) to the compass dimensions D_c estimated using the first point of the paths as a starting point for the compass algorithm. This result is fully consistent with previous investigations conducted on the 3-dimensional swimming trajectories of *Daphnia pulex* (Seuront et al. 2004b). Further, one may also note here that the compass dimension D_c estimated for males ($D_{c,m} = 1.15 \pm 0.05$, mean ± SD) and females ($D_{c,f} = 1.16 \pm 0.06$) is not significantly different (WMW test, $p > 0.05$) from the corresponding box-counting dimensions D (i.e. $D_m = 1.14 \pm 0.06$ and $D_f = 1.15 \pm 0.06$); see also Fig. 10.

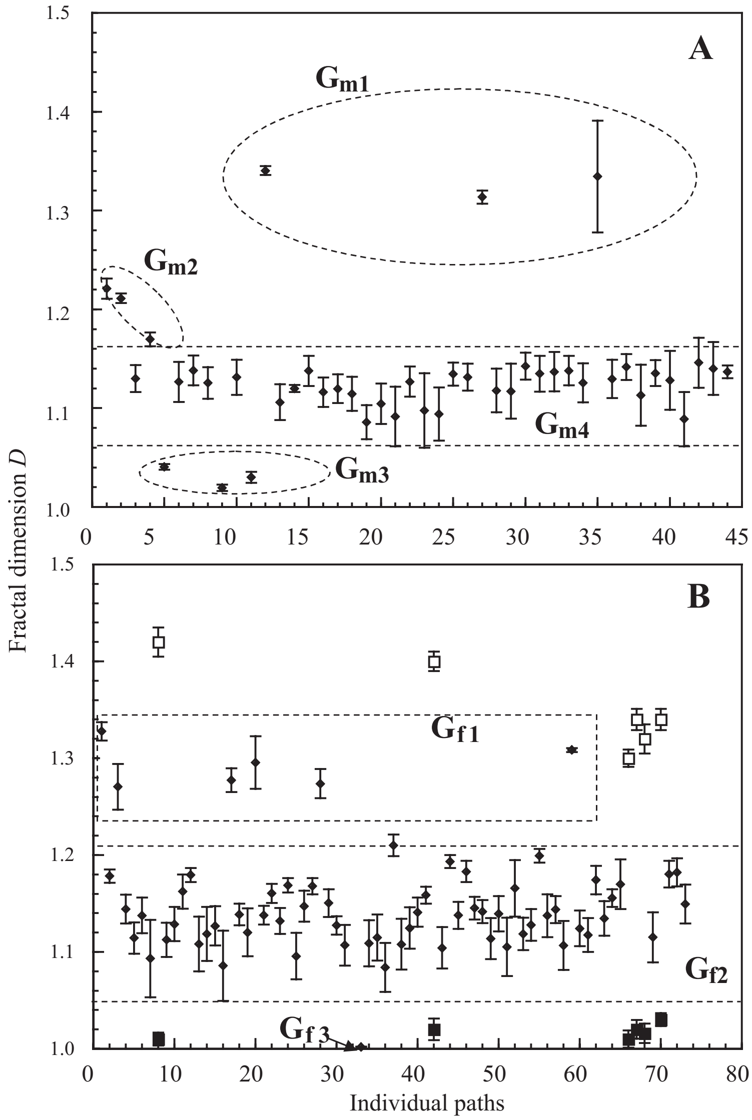

Fig. 9. *Oncaea venusta*. Fractal dimension D as a function of individual paths for males (A) and females (B). The black rhombi are the fractal dimensions estimated for male and female individual paths when scaling behavior occurred over the whole range of available scales. The open and black squares are the fractal dimensions estimated for the 6 female paths exhibiting 2 scaling behaviors for scales >10 and <10 mm (G10 group). Error bars are SD

In a study of the motion behavior of the marine snail *Littorina littorea*, Erlandson & Kostylev (1995) showed that the values of box-counting dimensions might be positively correlated to path length. This limitation of the box-counting method has been addressed by comparing the box-counting dimensions obtained from our 44 and 72 male and female swimming paths of different length. The resulting box-counting dimensions D' did not show any significant differences between the 126 available paths (covariance analysis, F-test, $p > 0.05$). These results thus ensure the relevance of our fractal dimension estimates.

Scale-dependent versus scale-independent metrics in behavioral studies

The intrinsic weakness related to the scale dependence of standard behavioral metrics (swimming speed and NGDR) has been discussed extensively in Seuront et

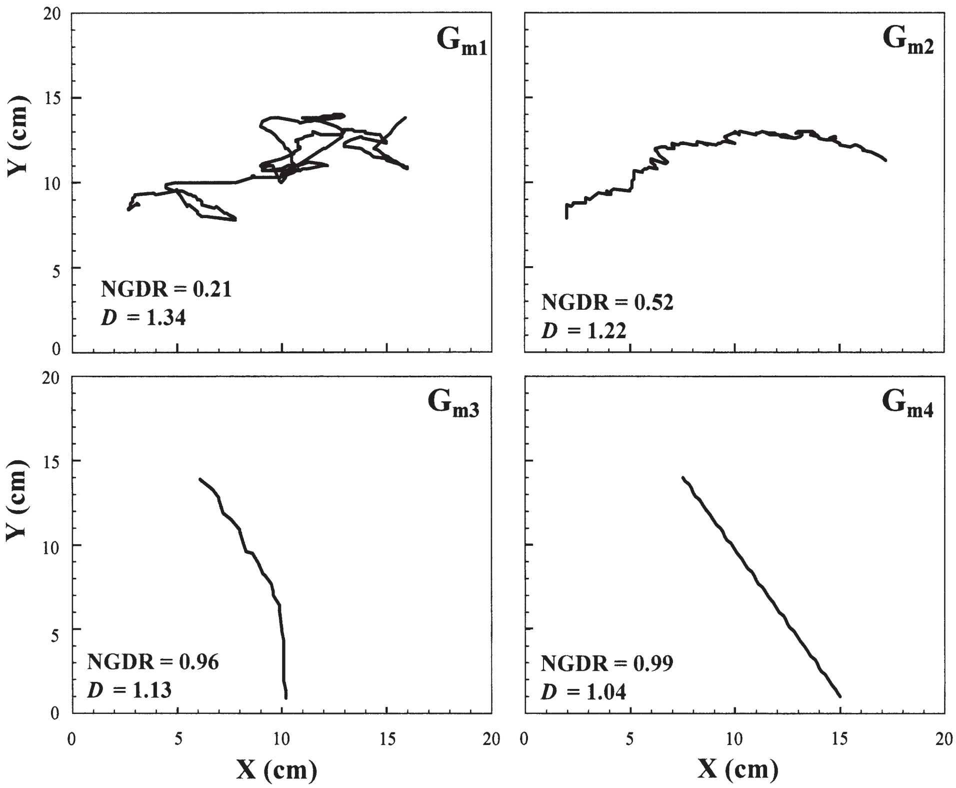

Fig. 10. *Oncaea venusta*. Illustration of the values taken by the net-to-gross displacement ratios (NGDR) and fractal dimension for swimming paths characteristic of the 4 distinct groups of behavior identified for males

al. (2004b). Here, we focused on the relevance of the differential information related to estimates of swimming speed, NGDR and fractal dimension, in terms of quantifying and classifying behavioral strategies. Fractal dimension thus appeared to be the most relevant behavioral metric for several critical reasons, aside from its scale-independent nature. First, fractal dimension is independent of the length of the swimming path (see Table 2), as previously suggested elsewhere (Seuront et al. 2004b). Second, the significantly lower intra- and inter-individual variability in fractal dimensions compared to swimming speed and NGDR suggests that the fractal dimension is more likely to identify slight differences in zooplankton behavior. This indeed seems to be the case here as fractal dimension allowed us: (1) to refine the initial qualitative, visual classification of swimming paths, e.g. the 'A-shaped' and 'V-shaped' swimming paths did not exhibit specific fractal properties, but were instead included in the G_{m3} and G_{f2} groups, (2) to identify, on the basis of objective statistical criteria, different groups of copepods within males and females (Figs. 11, 12) that could not have been distinguished using swimming speed and NGDR alone (compare Figs. 6, 9) and (3) to diagnose the presence of different levels of organization within an *a priori* rectilinear, swimming path (see Fig. 10 G_{m3} and G_{m4} and Fig. 11 G_{f3} and G_{10}). This is a desirable feature, as behavioral shifts in copepods relative to e.g. age (Van Duren & Videler 1995), mating (Van Duren & Videler 1996, Doall et al. 1998) and food quality and quantity (Tiselius 1992, Kiørboe et al. 1996), which can be limited to different combinations of hovering, hopping and cruising modes, were not necessarily detected using conventional behavioral metrics such as NGDR (Van Duren & Videler 1995, 1996, Tiselius 1992). In addition, the identification of 4 groups of swimming patterns for males and females investigated under the same laboratory conditions may suggest ontogenic differences in the food, light and temperature history of different groups or individuals. Further investigations are nevertheless needed to improve the relevance and to ensure the generality of the above arguments to other species of copepods, in different trophic and physical environments.

Zooplankton swimming and randomness

An important consequence of the fractal nature of zooplankton swimming behavior is its clear deviation from Brownian motion. Brownian motion, which can

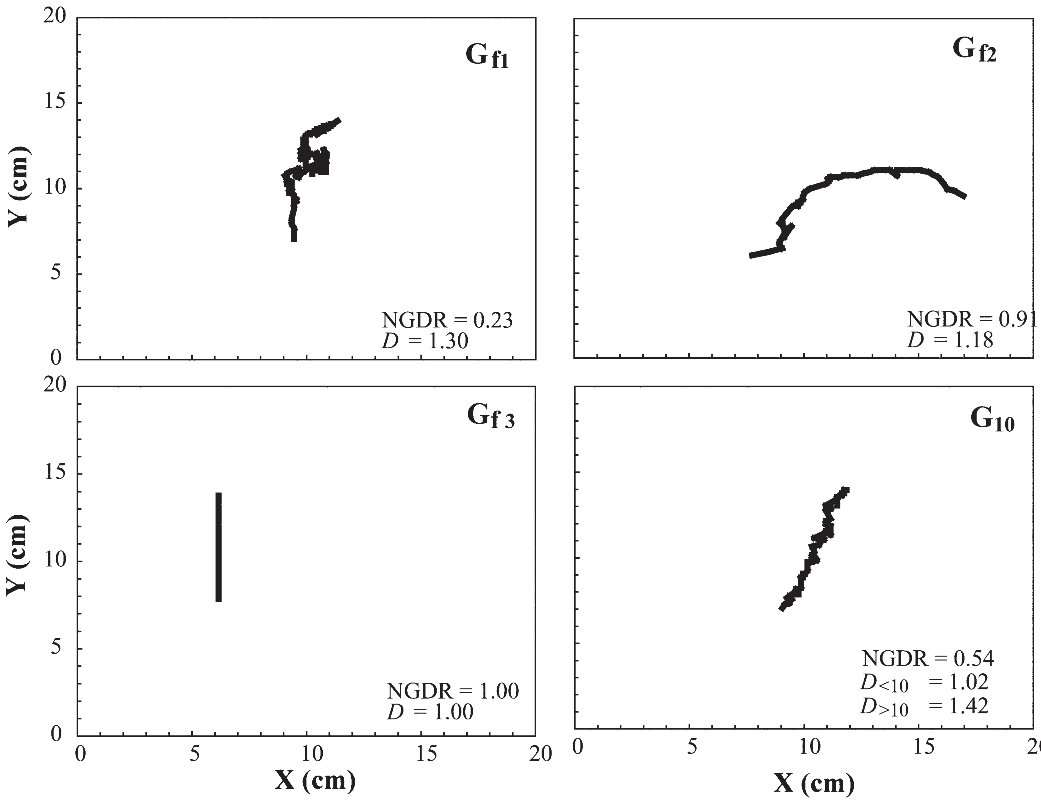

Fig. 11. *Oncaea venusta*. Illustration of the values taken by the NGDR and fractal dimension for swimming paths characteristic of the 4 distinct groups of behavior identified for females

be equivalently referred to as a normal diffusion process, is characterized by its space-filling properties and a related fractal dimension of D = 2.00. Brownian motion models have been suggested to characterize the movement of organisms (Berg 1983, Frontier 1987). However, Wiens & Milne (1989), examining beetle movements in natural fractal landscapes, found that observed beetle movements deviated from the modeled (Brownian) ones. Johnson et al. (1992) found that beetle movements reflect a combination of ordinary (random) and anomalous diffusions. To our knowledge all studies devoted to the study of the fractal behavior of freshwater and marine microzooplankton, zooplankton, or ichtyoplankton organisms never found any Brownian motion (Coughlin et al. 1992, Bundy et al. 1993, Brewer 1996, Jonsson & Johansson 1997, Dowl-

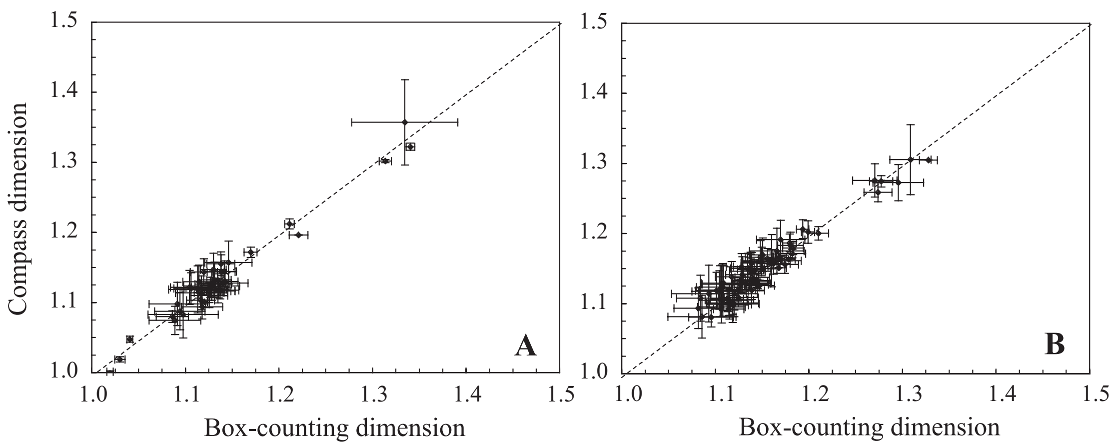

Fig. 12. *Oncaea venusta*. Comparison between the fractal dimensions obtained using the box-counting and the compass procedures, for males (A) and females (B)

ing et al. 2000, Schmitt & Seuront 2001, 2002, Bartumeus et al. 2003, Faure et al. 2003, Seuront et al. 2004a,b,c). This suggests that non-Brownian (or anomalous diffusion; see Schmitt & Seuront 2001, Seuront et al. 2004c) swimming could be the rule, rather than the exception, in aquatic ecology, as such strategies have been shown to be much more efficient than random motion in terms of foraging success (Viswanathan et al. 1999, Bartumeus et al. 2002).

The latter may simply reflect intrinsic departures from randomness, or result from barrier avoidance and utilization of corridors in natural landscapes. An extensive discussion of the anomalous (i.e. non-Brownian) diffusion of a copepod in a heterogeneous environment can be found elsewhere (Marguerit et al. 1998, Schmitt & Seuront 2001, 2002, Seuront et al. 2004c). Future modeling of zooplankton swimming behavior may thus have to take into account the non-randomness (i.e. fractal) of organisms' movements and the persistence of the direction of travel, as recently suggested by Schmitt & Seuront (2001), Wu et al. (1999) and Seuront et al. (2004c).

Ecological relevance of multiple-scaling behavior

Because different scales are often associated with different driving processes (Wiens 1989, Seuront & Lagadeuc 1997), the fractal dimension may have the desirable feature of only being constant over a finite, instead of an infinite, range of measurement scales. It is then useful for: (1) identifying characteristic scales of variability and (2) comparing movements of organisms that may respond, for instance, to the patchy structure of their environment at different absolute scales. Changes in the value of D with scale may indicate that a new set of environmental or behavioral processes are controlling movement behavior (e.g. decreased influence of patch barriers or the effect of home range behavior). Thus, the scale dependence of the fractal dimension over finite ranges of scales may carry more information, both in terms of driving processes and sampling limitation, than its scale independence over the whole range of available scales. In the present case, the observed change in fractal dimensions above and below a critical scale of 10 mm for group G_{10} is indicative of a combination of 2 distinct swimming modes operating at different spatial scales. As the fractal dimension of the swimming path for the scale >10 mm (D = 1.002 ± 0.001, mean ± SD) is not significantly different from the value expected in the case of strict linear swimming, D = 1.00, it could reasonably be related to a cruising mode. The more complex behavior observed for scales <10 mm (D = 1.42 ± 0.01) could thus be related to a microscale searching mode relative to local chemical and/or physical stimuli. As only 6 of the 72 females investigated here exhibited such a bimodal behavior, more experimental work is needed to investigate its origin.

While the occurrence of slope change may indicate the operational scale of different generative processes, it may also reflect the limited spatial resolution of the data being analyzed (Hamilton et al. 1992, Kenkel & Walker 1993, Gautestad & Mysterud 1994). However, as previously shown in *Daphnia pulex* trajectories (Seuront et al. 2004b, their Fig. 5), the effect of spatial resolution in the data will manifest itself as a gradual change of the fractal dimensions towards $D \rightarrow 1$ or $D \rightarrow 2$, and cannot be confused with a transition zone between 2 different scaling regions. What is critical for a proper interpretation of fractal dimensions is then to identify the range of scales over which the fractal dimension is invariant.

Zooplankton behavior and the structure of the environment

In light of the growing awareness of the scaling nature of marine ecosystems, in both their physical and biological aspects (e.g. Pascual et al. 1995, Seuront et al. 1996a,b, 1999, 2002, Seuront & Lagadeuc 1997, 1998, 2001, Seuront & Schmitt 2001, Lovejoy et al. 2001), it is becoming increasingly necessary to find a way to compare the composition of zooplankton swimming behaviors in relation to phytoplankton distributions. Considering the remote sensing ability of zooplankton, their behavior could be strongly influenced by the distribution of their phytoplankton prey. While, it is not yet possible to obtain 3-dimensional, microscale (i.e. scales < 1 m) distributions of phytoplankton cells in situ, it is feasible to obtain prolonged, simultaneous 1-dimensional records (i.e. vertical profiles and time series) of physical (shear, temperature, salinity) and biological (*in vivo* fluorescence, backscatter) parameters at scales of < 1 m (see e.g. Wolk et al. 2002, 2004). From such records, one may expect a 1-dimensional fractal dimension of phytoplankton distribution of D = 0.67 (Seuront & Lagadeuc 1997, Seuront et al. 2002). In the present study, we found 2-dimensional fractal dimensions D_{m} = 1.14 ± 0.06 and D_{f} = 1.15 ± 0.06 for males and females of *Oncaea venusta*, respectively. Unfortunately, a direct comparison of these 2 dimensions is not possible, because they characterize 2 processes embedded in different dimensions (Roy et al. 1987, Huang & Turcotte 1989, Seuront et al. 2004b). A more fundamental framework, the fractal codimension, has been introduced to make possible comparisons of the structure of patterns and processes embedded in different d-dimensional spaces. The fractal codimension c has been defined as:

$$c = d - D \quad (7)$$

where d is the Euclidean dimension of the embedding space and D the fractal dimension of the pattern/process under consideration (for ecological applications see Seuront et al. 1999, 2004b). The fractal codimension measures the fraction of the space occupied by the process of interest, and is bounded between $c = 0$ and $c = 1$ for 'standard' processes characterized by a fractal dimension D such as $d - 1 \leq D \leq d$. The fractal dimension D of swimming paths is intrinsically bounded between $1 \leq D \leq 2$, whatever the value of the embedded dimension d. For more generality we can thus consider a fractal codimension bounded between $c = 0$ and $c = d$. However, in such a framework, comparisons of codimensions estimated from processes embedded in different d-dimensional spaces are unfeasible without an *a priori* knowledge of the embedding dimension d. The fractal codimension subsequently provides only a relative measure of sparseness. The 'path codimension' c' (Seuront et al. 2004b):

$$c' = c/d \quad (8)$$

has thus been introduced as an absolute measure of sparseness. c' is bounded between $c' = 0$ for space-filling processes and $c' = 1$ for processes so sparse that their fractal dimension is nil, whatever the values of the original embedding dimensions d may be. The path codimensions of a phytoplankton distribution characterized by a fractal dimension of $D = 0.67$ is $c' = 0.33$. The path codimension of the swimming behaviors of males and females of *Oncaea venusta* are $c' = 0.430$ and $c' = 0.425$, respectively. The swimming behavior of *O. venusta* is thus less complex (or less space filling) than the distribution of its phytoplankton prey. In particular, this result fully agrees with studies demonstrating the differences in motility between predator and prey (e.g. Tiselius et al. 1993, 1997, Abraham 1998, Seuront & Lagadeuc 2001). However, *O. venusta* also feed on marine snow (Alldredge 1972), detritic materials (Yamaguchi et al. 2002), chaetognaths and appendicularians (Go et al. 1998). The swimming behavior of *O. venusta* might then be more complex than the distribution of phytoplankton cells; to confirm this, further behavioral investigations would be needed in the presence of the different food sources.

Consequences of fractal swimming behavior

The identification of 4 groups of males and females with significantly different fractal dimensions suggests that, within the same species, different individuals are susceptible to develop specific behavior in relation with local variability in e.g. food availability that may request enough behavioral plasticity to exploit very specific ecological niches such as those related to microzones and microscale patches (Mitchell et al. 1985, Azam 1998). According to the optimal foraging theory (Pyke 1984), zooplankton organisms are expected to optimize the energy required to capture a given amount of food. As the distance travelled between 2 points, and then the related energy expenditure, increases with increasing fractal dimensions, it could also be used as a foraging index. More generally, the path codimension provides a method of comparing the complexity of 2 interrelated processes, each of which may be embedded in a different dimensional space. Future investigations of zooplankton swimming behavior could thus take advantage of this method to systematically investigate the fractal nature of its prey to infer more detailed causality in predator–prey interactions.

Variability in zooplankton swimming behavior

According to the high intra- and inter-individual variability observed in the swimming paths of both males and females of the copepod *Oncaea venusta* (see Figs. 6, 9), it seems difficult to infer any causality in their behavior. However, some studies indicated that various species of *Oncaea* are omnivorous (Turner 1986). Although *O. venusta* can clearly feed on suspended motile cells (Turner & Tester 1989, Wu et al. 2004), *Oncaea* spp. are also known to feed on material attached to surfaces, such as marine snow (Alldredge 1972), and some authors have considered the genus *Oncaea* to be detritivore (Yamaguchi et al. 2002). On the other hand, Go et al. (1998) showed that *O. venusta* and 2 other congeneric species from the south of the Korean Peninsula can feed on much larger zooplankton species, such as chaetognaths and appendicularians. They showed that these species (*Oncaea* spp.) exhibit a complex swimming behavior when attacking chaetognaths. The observed variability in *O. venusta* swimming patterns could thus be related to the diversity of feeding modes characterizing this species. Further behavioral investigations, in particular on individuals fully acclimatized for several generations in the laboratory to specific food sources, are nevertheless needed to clarify this hypothesis.

Conclusions

The current study identified a challenging high intra- and inter-individual variability, probably related to the omnivorous feeding behavior of *Oncaea venusta*, that still needs to be investigated thoroughly.

In particular, one has to remember that this preliminary work does not address the potential differences in behavior between a still-water container in the laboratory and a real-world turbulent environment, where copepods must search for food while at the same time avoiding predation and finding a mate. We nevertheless clearly demonstrated that fractal analysis is a powerful tool to investigate thoroughly the intra- and inter-individual variability in zooplankton swimming behavior. In particular, fractal dimensions are less sensitive than standard behavioral metrics (swimming speed and NGDR) to technical and biological limitations, such as the number of available data points and individual variability. Individual swimming behavior is (1) the underlying mechanism generating population level behaviors, such as horizontal and vertical migration (e.g. Folt & Burns 1999); (2) likely to affect the outcome of predator–prey interactions, especially in the pelagic environment, where prey movement is important both as a cue to predators (Brewer & Coughlin 1995) and a determinant of encounter rate (Gerritsen & Strickler 1977); and (3) linked to individual feeding rates in most zooplankton species (Kiørboe et al. 1996, Caparroy et al. 1998), and we believe that the journey of 'behavioral fractals' to elucidate zooplankton behavior complexity is still in its infancy.

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