

Unravelling Plankton Behaviour: A Tribute to Rudi Strickler's Legacy and Innovations

Influence of egg sacs on the swimming performance of freshwater cyclopoid copepods

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ABSTRACT

Female cyclopoid copepods carry their embryos in egg sacs that impact swimming performance until nauplii hatch. We studied kinematic parameters and mechanical energy of small routine jumps and large escape jumps of non-egg-carrying (NEC) and egg-carrying (EC) females of *Mesocyclops leuckarti* and *Macrocyclus albidus*. The drag and body acceleration costs for EC females of *M. leuckarti* and *M. albidus* during routine jumps were 28 and 40%, respectively, higher than those for NEC females moving at the same speed. Maintaining position in the water column by small jumps was more costly for EC females, requiring 2.2–2.3 times more jumps and energy. Consequently, the persistence of EC females was limited in the open water. In *M. leuckarti* and *M. albidus*, the average speed and distances of jumps were 5–6 and 1.5–2.2 times higher, respectively, and the duration of jumps was 2.2–2.5 times shorter during escape than routine swimming. The maximum jumping speeds of NEC females, 40.6 and 50.5 cm s⁻¹, respectively, were 12–14% higher than those of EC females, whereas their power and cost of transport were 16 and 23% lower, respectively. These results clearly indicated that egg sacs impair swimming and increase energetic costs of movement.

KEYWORDS: *Mesocyclops leuckarti*; *Macrocyclus albidus*; swimming kinematics and energetics; filming

INTRODUCTION

Reproduction is a primary life aspect. Copepods reproduce either as broadcast (i.e. free spawners) releasing their eggs into the surrounding water or carry their eggs (i.e. sac spawners) until nauplii hatch from one or two egg sacs attached to the abdomen (Barth-Jensen *et al.*, 2020). Calanoid copepods show both reproductive strategies, whereas cyclopoid copepods are exclusively sac spawners (Logerwell and Ohman, 1999). Free and sac spawners typically have different maximum fecundity and egg mortality rates as well as different egg hatching times. In broadcast spawners, the high egg production and short egg hatching time is an adaptation to the high mortality of freely spawned eggs, whereas sac-spawners have a low fecundity because of the low mortality of carried eggs (Kjørboe and Sabatini, 1994). While carried eggs show a low mortality, the egg sacs hinder the locomotion of egg-carrying (EC) females and consequently increase energy requirements and decrease the predator escape ability and foraging efficiency (Koehl, 2023). Specifically, EC females of some calanoid copepods have lower swimming speeds and have therefore a higher mortality risk by predation than non-egg-carrying (NEC) females (Svensson, 1992; Maier *et al.*, 2000; Seuront, 2006, 2013). EC females of the calanoid *Pseudocalanus elongatus* have a 1.3 times lower speed during escape swimming than NEC females and show a higher energy expenditure by about 17% because of dragging

the egg sac (Svetlichny *et al.*, 2017). Similarly, dragging the egg sac increases the total metabolic energy expenditure in calanoid females of *Calanipeda aquaedulcis* and *Arctodiaptomus salinus* by 32.7 and 25.7%, respectively (Svetlichny *et al.*, 2012b). The predation efficiency of fish is three times greater on EC females of *Cyclops vicinus* than on NEC females because egg sacs impair the copepod's acceleration and maneuverability (Winfield and Townsend, 1983). Cyclopoids have a higher predation risk than calanoids because the lateral or dorsal position of cyclopoid egg sacs impedes escape swimming more than the ventral position of calanoid egg sacs (Logerwell and Ohman, 1999). Despite the evident importance of the egg sac for copepod swimming, experiments on swimming efficiency are usually carried out with NEC individuals (e.g. Strickler, 1975, 1977; Strickler and Balàzsi, 2007; Buskey, 1998; Buskey *et al.*, 2002; Jiang and Kjørboe, 2011 and many others). Only few experimental studies confirm the effect of egg sacs on swimming in cyclopoid copepods (Kjørboe *et al.*, 2010a).

This study fills this knowledge gap by experimentally testing if and how egg sacs affect the kinematic parameters and energy efficiency of cruising and escape swimming in females of two different-sized cyclopoid species, namely, *Mesocyclops leuckarti* and *Macrocyclus albidus*. Considering the high frequency of jumps of freshwater copepods during swimming, a detailed kinematic and hydrodynamic analysis of the swimming behavior

and energetic costs of NEC and EC females using high-speed video recording was performed. This study also provides a detail description of the escape response of the two species stimulated by non-damaging electrical impulses.

METHODS

Copepods collection

Individuals of the cyclopoid copepods *M. leuckarti* and *M. albidus* were collected with a plankton net (mesh size: 100 μm ; mouth diameter: 0.3 m) in an artificial pond of the Orekhovotka river (Kyiv) in early autumn 2022. On average, 10–15 active EC and NEC females of *M. leuckarti* and five EC and five NEC females of *M. albidus* were selected for behavioral experiments. Before the experiment, females were acclimated (24 h at 22°C) to laboratory conditions in separate 1-L aquaria filled with filtered and aerated water and were fed with a small amount of natural microplankton (<100 μm).

Behavioral experiments

Copepod behavior was filmed using a Nikon 1J5 (Japan) camera equipped with Macro Bellows and a long-focus lens (LOMO Microplanar 4.5/100 mm; USSR). Two different experimental settings were used: (i) two to three females of each species and reproductive state (i.e. EC and NEC females) were placed in a small aquarium (length \times width \times height = 50 \times 20 \times 50 mm) and filmed at low light and 60 frames per second (fps) with resolution 1920 \times 1080 pixels for 30 s in three replications to determine the jump frequency and average traveling speed during routine relocation swimming; (ii) two to three females of each species were placed in a small aquarium (length \times width \times height = 20 \times 7 \times 30 mm) with a millimeter grid on the side wall and filmed at 1200 fps with resolution 440 \times 144 pixels, a shutter speed of 1:16000 and a shooting scale (i.e. the size ratio between the object's real size and its size on the image focused on the camera matrix) of 1:3 to 2:1 for 3 s. The large focal length of the lens (100 mm) and the distance between the camera matrix and the lens focusing point (up to 500 mm) provided a depth-of-focus of about 6 mm at aperture number f/16 and a video scale of 1:1. Thus, the image of copepods was almost always sharp, since the internal width of the narrow part of the rectangular vessel was 7 mm. At least 20 replications were used to study the kinematic structure of jumps during routine relocation swimming and escape reaction performed by separate jumps and by continuous series of jumps, respectively. Specifically, the duration, distance and instantaneous speed during the stroke and return phases of a jump and mean kinematic parameters of a total jump, comprising the stroke and return phase, were assessed. Illumination of the aquarium was provided by a bright diffuse backlight created with a shaded 10-W LED illuminator (light intensity of about 2000 lux). Short electrical impulses (9-V battery) were used to stimulate the escape reaction as already done with the freshwater cyclopoid copepod *C. vicinus* (Svetlichny and Obertegger, 2022). While non-damaging electrical impulses cause a stable escape reaction in many marine and freshwater copepods (Svetlichny, 1986, 1987; Svetlichny *et al.*, 2022; Svetlichny and Obertegger, 2022), mechanical and light stimulation (Buskey *et al.*, 2002; Buskey and Hartline, 2003;

Burdick *et al.*, 2007; Waggett and Buskey, 2008; Kiørboe *et al.*, 2010b) very rarely evoked a full-fledged escape response in *M. leuckarti* and *M. albidus* (own observation).

Only video fragments showing the movements of specimens in the focal plane of the camera were used for frame-by-frame analysis using VirtualDub (<http://www.virtualdub.org/index>). For all types of swimming, the instantaneous speed (U_i) in cm s^{-1} was calculated at inter-frame time of 0.000833 s as $U_i = hi \cdot 0.000833^{-1}$, where hi is the inter-frame straight-line change of the geometric center position of the copepod prosome.

Body measurements

The total length (L_{tot} , cm) and the length and width of the prosoma (l_{pr} and d_{pr} , cm) were measured of anesthetized females after the conclusion of the experiments. Females were anesthetized according to Svetlinchy and Obertegger (2023). Body volume (V_b , cm^3) was calculated using equation $V_b = 0.47 \cdot 10^{-3} \cdot L_{\text{tot}}^{0.21} \cdot l_{\text{pr}}^{0.93} \cdot d_{\text{pr}}^{1.86}$ with an accuracy of 9.8% for female cyclopoid species (Svetlichny *et al.*, 2012a, supplement). Wet mass (M , g) was calculated using equation $M = V_b \cdot \rho_b$, with body density $\rho_b \approx 1.05 \text{ g cm}^{-3}$ (Mauchline, 1998). The volume and weight of egg sacs were calculated from the diameter and number of eggs in both sacs of EC females.

Energetic cost of swimming

The mechanical energy of jumps (E_{jump} , J) was estimated by the equation $E_{\text{jump}} = 2 \cdot (E_{\text{drag}} + E_{\text{kin}})$. E_{drag} and E_{kin} are the energy required to overcome drag and acceleration of the body, respectively. The Factor 2 is based on the fact that in aquatic arthropods moving occurs because of strokes with oar-shaped limbs according to the principle of action of first-class levers, the arms of which are the body and remote, bristly segments of the legs. At each moment the body moves forward, the distal ends of the legs move backward relative to a fixed point in space, which was first noticed by Nachtigall (1974). According to the law of energy conservation, the same amount of work is done on both sides of such a body–limbs lever system.

E_{drag} of one jump was calculated by the equation $E_{\text{drag}} = H \cdot R_{\text{drag}}$, where H is the distance of one jump (cm) and R_{drag} is the drag force (dyne) determined by the equation $R_{\text{drag}} = 0.5 \cdot C_d \cdot \rho_w \cdot S_{\text{body}} \cdot U^2$. C_d is the drag coefficient, and ρ_w is water density (g cm^{-3}). S_{body} is the body cross-section area (cm^2), determined as $S_{\text{body}} = 0.25 \cdot \pi \cdot d_{\text{pr}}$. U is mean swimming speed (cm s^{-1}). The drag coefficient was calculated using the empirical equations of their dependence on the Reynolds number (Re) as $C_d = c \cdot \text{Re}^{-0.74}$ at Re between 1 and 20 and $C_d = c \cdot \text{Re}^{-60}$ at Re between 1 and 1200 (Svetlichny *et al.*, 2020). $\text{Re} = d_{\text{pr}} \cdot U / \nu$, where ν is kinematic viscosity ($\text{cm}^2 \text{ s}^{-1}$). The hydrodynamic body shape coefficient c for NEC females was determined in accordance with its empirical dependence on body elongation ($l_{\text{pr}}/d_{\text{pr}}$) of cyclopoid and calanoid copepods (Svetlichny, 1983). In accordance with the $l_{\text{pr}}/d_{\text{pr}}$ ratio of the studied species (*M. leuckarti*: 1.5; *M. albidus*: 1.7), c values were 48 and 32 for moving at Re between 1 and 20 and between 20 and 1200, respectively. In EC females, the length-to-width ratio of the body with attached egg sacs was approximately twice as large as in individuals without egg sacs; therefore, the coefficients

Table I: Morphological characteristics of female *M. leuckarti* and *M. albidus*; number of observations (*nr*); different letters indicate significant differences at $P < 0.001$

Parameters	<i>M. leuckarti</i>	<i>M. albidus</i>
nr	31	7
Total length, cm	0.149 ± 0.0048 ^a	0.183 ± 0.0070 ^b
Prosome length, cm	0.083 ± 0.004 ^a	0.110 ± 0.0047 ^b
Body width, cm	0.049 ± 0.0018 ^a	0.074 ± 0.0039 ^b
Number of eggs in both egg sacs	100.8 ± 20.3 ^a	49.3 ± 10.6 ^b
Body volume, mm ³	0.117 ± 0.0126 ^a	0.333 ± 0.0433 ^a

c taken for EC females were 80 and 48 for moving at Re between 1 and 20 and between 20 and 1200, respectively.

E_{kin} of one jump was calculated using the equation $E_{kin} = 0.5 * (M + m) * (U_{max}^2 - U_{min}^2)$, where m is added mass, which is for a prolate ellipsoid $< 10\%$ of M as approximation to the studied cyclopoid copepods with the total body aspect ratio $L_{tot}/d_{pr} \approx 2.5-3$ (Daniel, 1984; Vogel, 1994). We also did not take into account the influence of the vessel walls on the speed of movement of copepods, since it has experimentally been shown in cylindrical tubes that vessel walls do not affect the speed of movement at $Re > 10$, if the distance between the vessel walls exceeds 10 times the body diameters of individuals with antennules pressed to the body (Stepanov and Svetlichny, 1981). These conditions applied to our experiments.

Statistics

Data analyses and representation were carried out with the software Grapher (v.19) of Golden Software programs and R 4.3.0 (R Core Team, 2023). A t -test was applied to investigate morphological differences between species (*M. leuckarti* and *M. albidus*) irrespective of the reproductive status, except for the number of eggs in the egg sacs. A two-way ANOVA was used to test for differences between kinematic swimming parameters using species (*M. leuckarti* and *M. albidus*) and reproductive status (EC and NEC females) as factors. We analyzed differences between routine and escape swimming (distance, duration, minimum, maximum and mean speed) separately for each species by a two-way ANOVA using swimming type (small relocation jumps, escape swimming) and reproductive status (EC and NEC females) as factors. Linear regression was used to investigate the dependence of swimming speed of the two species on swimming duration of different swimming types (small relocation jumps, escape swimming). We used ANOVA results from library car (Fox and Weisberg, 2019), appropriate for the unbalanced sampling design. In all analyses except for morphology, identity of individuals was used as random factor and their parameters inferred using library lme4 (Bates et al., 2015) because individuals (5–10) were filmed several times. Post hoc comparisons were performed with library emmeans (Lenth, 2023) considering multiple testing by applying Tukey's correction. Values presented in tables are means ± 1 SD.

RESULTS

Morphology

Females of *M. leuckarti* (from here on Mesocyclops) were smaller (Table I; Fig. 1) than females of *M. albidus* (from here on

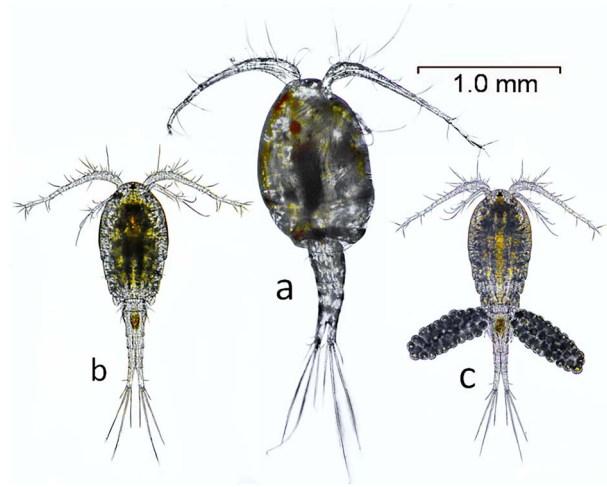


Fig. 1. NEC female of *M. albidus* (a) and NEC (b) and EC (c) female of *M. leuckarti*.

Macrocyclus). However, EC females of Mesocyclops carried generally more eggs than Macrocyclus (Table I).

Characteristics of the small relocation jumps

Small jumps, with which specimens perform all the functions associated with routine movement such as search and capture of food, were the main behavior type of the studied cyclopoid copepods (Fig. 2). The jump–sink behavior type usually alternated with a series of small jumps (Fig. 3a). During the stroke phase of small jumps, EC females pressed the eggs to the abdomen so that the general shape of the body took the form of an elongated ellipsoid. In contrast, while resting before jumping, egg sacs were located at a large angle to the body axis (up to 60°) in Mesocyclops and at much smaller angular amplitude (not more than 45°) in Macrocyclus. During the phase of each small jump during cruising, the body of NEC females of Macrocyclus initially accelerated to a maximum speed of 12.2 cm s⁻¹. Then, the speed slightly decreased despite the power stroke of the first pair of legs and sharply decreased to 1.6–2.8 cm s⁻¹ during the return movement of all limbs and antennules. Finally, speed decreased to 0.7–1.2 cm s⁻¹ during the phase of complete rest between jumps until the next jump began. NEC females of Mesocyclops showed a similar speed and angular displacement of swimming legs as Macrocyclus. Specifically, Mesocyclops initially accelerated to a maximum speed of 11.5 cm s⁻¹ and reached a minimum speed of 0.3 cm s⁻¹ until the next jump began.

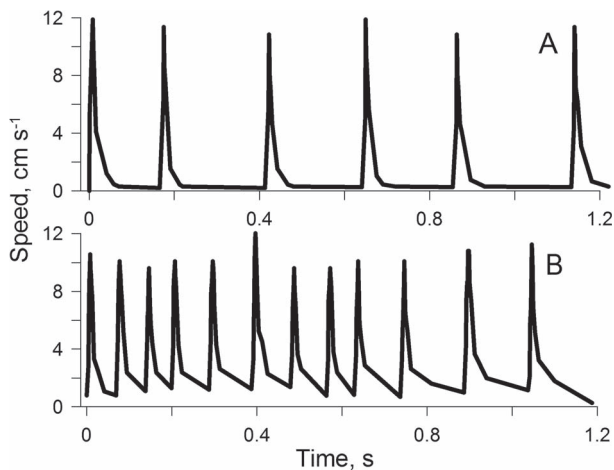


Fig. 2. Example of instantaneous speed dynamics during cruising by small jumps in NEC females of *M. leuckarti* (a) and *M. albidus* (b).

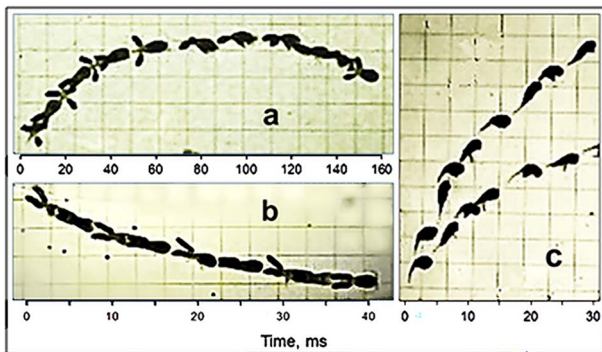


Fig. 3. Swimming patterns of *M. leuckarti*. Panels a and b show sequences of images corresponding to changes in body position in real scale during the stroke and recovery phase of the jump in EC female, to visualize changes in the angular position of the body and egg sacs during small relocation jumps and escape reaction, respectively. Panel c shows the image sequences during the stroke and return phase of the escape jumps of two NEC females. Length and width of the background coordinate grid is 1×1 mm.

For both species, the deviation of the body axis relative to the direction of movement in the stroke and back phases of the jump did not exceed $40\text{--}50^\circ$. NEC and EC females of *Mesocyclops* and *Macrocyclus* show similar movement patterns during small jumps. The average distances, duration and the average speed during single jumps or a series of routine jumps were similar in both species, irrespective of the reproductive status (Table II). However, the maximum instantaneous speed of NEC females was larger than that of EC females ($P < 0.001$), irrespective of species (Table II). The average jump frequency of EC females was 1.4 times higher ($P < 0.001$) than that of NEC females for *Mesocyclops* while not for *Macrocyclus* (Table II). The average traveling speed taking into account pauses between jumps, on the contrary, was 1.6 and 1.3 times, respectively, higher in EC females ($P < 0.001$) than in NEC females of *Mesocyclops* and *Macrocyclus*. Furthermore, *Macrocyclus* showed generally a higher average traveling speed ($P < 0.001$) than *Mesocyclops* (Table II).

For both species, duration, distance and speed (mean, maximum, minimum) showed higher values ($P < 0.001$) with escape

swimming than with routine jumps. In both species, the sinking speed during long periods between jumps was 1.5 times greater ($P < 0.01$) in EC females than in NEC females (Table II). While the jump distance varied widely from 0.04 to 0.16 cm in *Mesocyclops* and from 0.05 to 0.18 cm in *Macrocyclus*, jump speed was dependent on jump duration ($P < 0.001$) (Fig. 4a).

Escape reaction

In the studied cyclopoid species, as in all free-swimming copepods, the escape reaction was composed of continuous series of jumps (Figs 3b and c and 5). On straight sections of the movement trajectory, the deviation of the body axis relative to the direction of movement in the stroke and back phases increased in both species to $60\text{--}80^\circ$ (Figs 3c and 6). The average distance of escape jumps was higher in NEC females than in EC females, irrespective of species (Table II). The average duration of escape jumps was similar between NEC and EC females in *Mesocyclops* but was higher in EC females of *Macrocyclus* (Table II). The average duration and the average speed of escape jumps were 3.4–4.4 times smaller and were 5–6.2 times greater, respectively, than that of routine jumps (Table II). The duration of the stroke phases of escape jumps was 55–65% of their total duration (~ 0.011 s), and therefore the speed of movement during the shorter period when limbs returned to their initial position (about 0.004 s; i.e. the preparation for the next jump) could not decrease as much (Fig. 5) as in routine jumps (Fig. 2). Consequently, the initial speed of each subsequent jump, except for the first jump, in the series of escape jumps was on average 3 and 2.4 times less than the maximum speed during the acceleration phase of NEC females of *Mesocyclops* and *Macrocyclus*, reaching 40.6 and 50.5 cm s^{-1} , respectively. The maximum and minimum jump speed of NEC females of both species were higher ($P < 0.001$) than in EC females (Table II). Only in *Macrocyclus*, however, was the average speed of the entire escape reaction ($P < 0.05$) 15% higher in NEC females than in EC females. Total jump duration was not different between species, irrespective of the female reproductive status. In both species regardless of the female reproductive status, the mean speed of escape jumps was dependent on jump duration ($R^2 = 0.48$ and 0.56 ; Fig. 4b).

Mechanical energy of small routine and escape jumps

The average mechanical power of routine jumps of NEC females of *Mesocyclops* and *Macrocyclus* was 1.5 times smaller than that of EC females (Table III). The mechanical power of escape jumps in NEC females of *Mesocyclops* and *Macrocyclus* was 53 and 67 times higher than the average power of routine jumps. Furthermore, the power required to perform the escape jumps was higher by 1.2 and 1.3 times in EC females, respectively, than in NEC females.

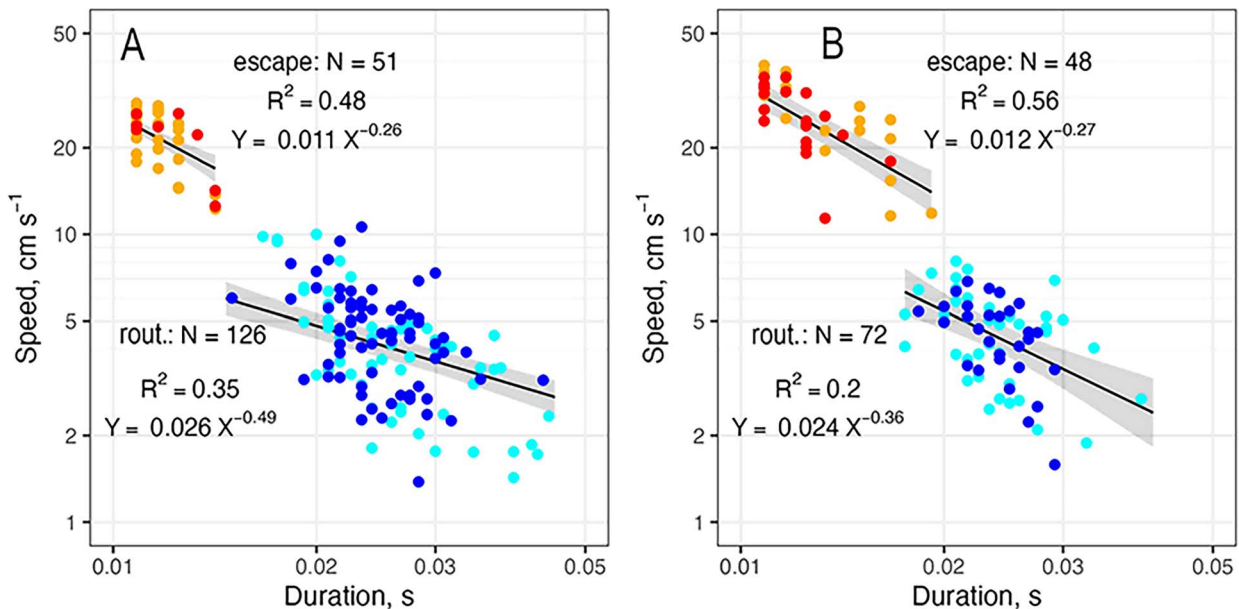
DISCUSSION

Swimming types

Although many studies have focused on cyclopoid copepod swimming (e.g. Strickler, 1975, 1977; Alcaraz and Strickler, 1988; Morris *et al.*, 1990; Buskey *et al.*, 1996; Kiørboe *et al.*, 2010a), parameters for routine and escape jumps are generally

Table II: Kinematic parameters of swimming in *M. leuckarti* and *M. albidus*; different letters indicate significant differences considering species identity as random factor in two-way ANOVA (species and reproduction type as factors)

Parameters	<i>M. leuckarti</i>		<i>M. albidus</i>	
	NEC females	EC females	NEC females	EC females
Small relocation jumps				
nr	61	68	42	31
Distance, cm	0.107 ± 0.037 ^a	0.114 ± 0.04 ^a	0.117 ± 0.039 ^a	0.105 ± 0.028 ^a
Duration, ms	26.7 ± 7.0 ^a	25.0 ± 4.4 ^a	23.7 ± 4.3 ^a	24.2 ± 2.7 ^a
Mean speed, cm s ⁻¹	4.4 ± 2.4 ^a	4.7 ± 1.8 ^a	5.1 ± 2.1 ^a	4.4 ± 1.3 ^a
Minimum speed, cm s ⁻¹	0.3 ± 0.12 ^a	0.3 ± 0.16 ^a	1.0 ± 0.23 ^b	0.8 ± 0.25 ^b
Maximum speed, cm s ⁻¹	11.5 ± 0.92 ^a	10.6 ± 1.77 ^b	12.2 ± 2.77 ^a	10.3 ± 0.72 ^b
Jump frequency during traveling	6.2 ± 2.24 ^a	9.6 ± 3.29 ^b	7.3 ± 2.48 ^a	8.4 ± 1.43 ^b
Traveling speed, cm s ⁻¹	0.7 ± 0.24 ^b	1.1 ± 0.37 ^a	1.1 ± 0.39 ^a	1.4 ± 0.40 ^c
Sinking speed, cm s ⁻¹	0.3 ± 0.07 ^a	0.5 ± 0.18 ^{bc}	0.3 ± 0.11 ^{ac}	0.5 ± 0.18 ^b
Frequency of jumps to overcome gravity, Hz	3 ± 0.9 ^a	4 ± 1.7 ^b	3 ± 1.7 ^a	5 ± 2.4 ^b
Escape jumps				
Nr	34	14	27	26
Stroke phase distance, cm	0.26 ± 0.042 ^a	0.25 ± 0.041 ^b	0.36 ± 0.038 ^c	0.31 ± 0.055 ^d
Stroke phase duration, ms	6.1 ± 0.55 ^a	6.2 ± 0.63 ^{ab}	6.7 ± 0.78 ^b	7.2 ± 0.78 ^c
Stroke phase mean speed, cm s ⁻¹	32.3 ± 6.65 ^{ad}	27.6 ± 4.65 ^b	37.9 ± 5.22 ^c	32.8 ± 6.84 ^d
Minimum speed, cm s ⁻¹	13.7 ± 4.95 ^a	9.5 ± 2.73 ^b	21.4 ± 4.87 ^c	17.5 ± 5.56 ^d
Maximum speed, cm s ⁻¹	40.6 ± 4.07 ^a	36.2 ± 7.59 ^b	50.5 ± 6.02 ^c	44.1 ± 7.87 ^{da}
Total jump distance, cm	0.27 ± 0.042 ^a	0.25 ± 0.041 ^b	0.36 ± 0.038 ^c	0.31 ± 0.055 ^d
Total jump duration, ms	11.1 ± 1.0 ^a	11.0 ± 0.001.8 ^a	11.6 ± 2.1 ^a	11.6 ± 1.6 ^a
Total mean speed, cm s ⁻¹	24 ± 4.0 ^a	23 ± 4.5 ^a	32 ± 5.3 ^b	28 ± 6.2 ^a

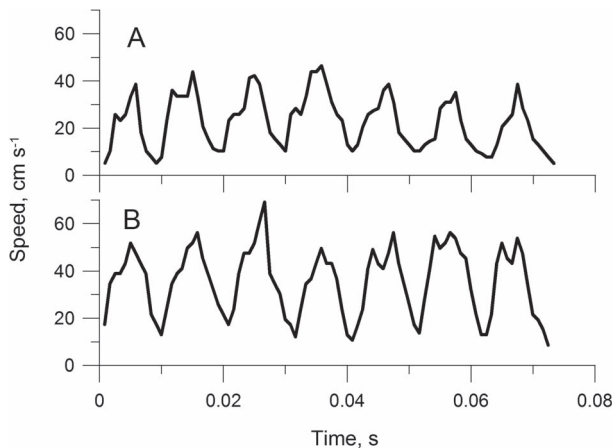
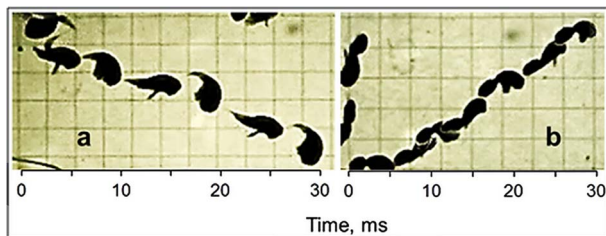
**Fig. 4.** Regression of mean speed dependent on the jump duration for small routine jumps (rout.; blue circles for EC and cyan circles for NEC females) and escape jumps (red circles for EC and orange circles for NEC females) of *Mesocyclops leuckarti* (A) and *Macrocyclus albidus* (B); identity of specimens was used as random factor in linear modelling, and the gray shaded area is the 95% confidence interval of the regression.

not distinguished, providing a biased understanding on swimming dynamics and efficiency. Specifically, routine swimming of cyclopoid copepods (i.e. *C. vicinus*, *Thermocyclops oithonoides*, *Oithona davisae*) is characterized by one or two to three successive jumps or series of separate jumps during a long

cruising movement, during which the swimming legs, especially the first pair of thoracic legs, make strokes with reduced angular amplitude, and the antennules return to their original position after each separated jump (Svetlichny *et al.*, 2022; Svetlichny and Obertegger, 2022). In contrast, the escape reaction consists

Table III: Energy characteristics of jumps in *M. leuckarti* and *M. albidus* taking mean values for swimming parameters and body mass

Parameters	<i>M. leuckarti</i>		<i>M. albidus</i>	
	NEC females	EC females	NEC females	EC females
Mean body mass, mg	0.12	0.15	0.35	0.41
Routine jumps				
E_{total} , total energy of one jump, J	$3.54 \cdot 10^{-9}$	$5.46 \cdot 10^{-9}$	$9.28 \cdot 10^{-9}$	$9.8 \cdot 10^{-9}$
E_{drag} , energy dissipation by drag, % of total	55	69	47	55
E_{kin} , kinetic energy, % of total	45	31	53	45
P , power, W	$1.3 \cdot 10^{-7}$	$2.18 \cdot 10^{-7}$	$3.87 \cdot 10^{-7}$	$4.08 \cdot 10^{-7}$
P_m , mass-specific power, W kg^{-1}	1.09	1.82	1.17	1.2
Cost of transport, $\text{cal g}^{-1} \text{m}^{-1}$	$5.9 \cdot 10^{-3}$	$8.2 \cdot 10^{-3}$	$4.4 \cdot 10^{-3}$	$7.4 \cdot 10^{-3}$
Power to overcome gravity, W	$9.5 \cdot 10^{-9}$	$2.07 \cdot 10^{-8}$	$2.4 \cdot 10^{-8}$	$5.6 \cdot 10^{-8}$
Escape reaction				
E_{total} , total energy of one jump, J	$7.62 \cdot 10^{-8}$	$9.03 \cdot 10^{-8}$	$2.55 \cdot 10^{-7}$	$3.35 \cdot 10^{-7}$
E_{drag} , energy dissipation by drag, % of Total	74	80	73	60
E_{kin} , kinetic energy, % of total	26	20	27	40
P , power, W	$6.93 \cdot 10^{-6}$	$8.21 \cdot 10^{-6}$	$2.19 \cdot 10^{-5}$	$2.89 \cdot 10^{-5}$
P_m , mass-specific power, W kg^{-1}	57.8	68.4	62.6	82.6
Cost of transport, $\text{cal g}^{-1} \text{m}^{-1}$	$57.5 \cdot 10^{-3}$	$70.2 \cdot 10^{-3}$	$47.3 \cdot 10^{-3}$	$70.7 \cdot 10^{-3}$

**Fig. 5.** Instantaneous swimming speed of NEC females of *M. leuckarti* (a) and *M. albidus* (b) during escape reaction.**Fig. 6.** Swimming patterns and changes in body shape and position of *M. albidus* for NEC females (a) and EC females (b) during escape reaction. The scale of the background coordinate grid is 1×1 mm. It can be seen that the deviations of the body during the movement of females carrying eggs become more aligned because of the fact that the egg sacs are attached to the back of the body.

of continuous series of jumps without pauses, during which the antennules are constantly pressed against the body, and the limbs and abdomen perform forceful strokes with the

maximum possible angular amplitude and speed (Svetlichny *et al.*, 2022; Svetlichny and Obertegger, 2022). Here, the two different-sized cycloids *M. leuckarti* and *M. albidus* also showed a clear difference between routine and escape swimming (Supplementary Material, Videos S1 and S2) with the average speeds and distances of jumps being 5–6 and 1.5–2.2 times lower, respectively, and the duration of jumps being 2.2–2.5 times longer during routine swimming than during escape swimming. Furthermore, the maximum speed of the escape reaction in females of *M. leuckarti* and *M. albidus* (40.6 and 50.5 cm s^{-1} , respectively) corresponded to the maximum swimming speeds of other copepods with the same body size (Buskey *et al.*, 2002; Buskey and Hartline, 2003; Burdick *et al.*, 2007; Waggett and Buskey, 2008; Kjørboe *et al.*, 2010b).

Routine swimming

In addition to the usual phases of acceleration and deceleration during the power and return phases of movement of the body appendages, *M. leuckarti* and *M. albidus* showed an inertial movement after the completion of jumps during routine swimming. A similar inertial movement is often observed in large copepods and has been described in detail in *T. oithonoides* (Svetlichny *et al.*, 2022) and *C. vicinus* (Svetlichny and Obertegger, 2022). Here, the larger *M. albidus* also had a more pronounced inertial movement than *M. leuckarti*, as indicated by the higher minimum speed during the phase of complete rest between jumps. Because of this inertial effect, the almost 2-mm long *M. albidus* keeps moving even in the pauses between jumps. For example, during one of the fastest horizontal cruising movements with an average speed of 1.99 cm s^{-1} , after making 12 jumps within 1.19 s (Fig. 2b), NEC females of *M. albidus* moved 2.4 cm of which almost half the distance (1.1 cm) was traveled by inertia. Since the total duration of power strokes creating water disturbance was $<10\%$ of the total duration of the cruising movement, it can be assumed that such movements are less perceptible by predators stimulated by the hydrodynamic signal of their prey (Kjørboe *et al.*, 2010a),

Interestingly, although egg sacs increased female weight by 20 and 15% in *M. leuckarti* and *M. albidus*, respectively, speed, distance and duration of single routine jumps were not different between NEC and EC females. However, during traveling in a rectilinear movement from one side to the other of the small aquarium (length = 50 mm), jump frequency of EC female of *M. leuckarti* and *M. albidus* was significantly higher than that of NEC females. This was probably because of the greater sensitivity of EC females to the experimental setting. Having completed this movement, EC females often attached to the walls of the vessel or near the bottom. Considering such pauses, the jump frequency of *M. leuckarti* could vary widely from 1 to 53 jumps m^{-1} , whereas in *M. albidus* it ranged from 66 to 168 jumps m^{-1} . Under natural conditions these copepods will most probably exhibit even less locomotor activity. For example, *M. leuckarti* attached to the surface film of the water and often stayed immobile in the large 5-L aquarium for several minutes unless stimulated by external stimuli. Because of their widely spaced egg sacs, their silhouette was clearly visible in the water to the human eye and, perhaps, also to predators feeding in the hyponeustonic layer. Like many large freshwater cyclopoid copepods, individuals of *M. albidus* live near the bottom of littoral zones or in shallow water bodies (Tinson and Laybourn-Parry, 1986; Gaponova, 2019), where they can also stay motionless. To estimate how active a species must be to stay in the water column, we calculated the frequency of jumps that would allow them to compensate for gravitational sinking (Table I). EC females of *M. leuckarti* and *M. albidus* must perform vertical jumps with frequencies of 3.8 and 4.9 Hz, whereas NEC females must jump only with 2.7 and 3.0 Hz, respectively. Although this jump frequency seems too high for a normal copepod behavior, some species maintain such a high locomotor activity for several hours. For example, freshwater *T. oithonoides* performs routine jumps for a long time at a frequency of 1.9 to 3.4 Hz at 20°C (Svetlichny et al., 2022). Also *C. vicinus* females jump for a long time at a frequency of about 3.0 and 4.5 Hz in low and bright light, respectively (Svetlichny and Obertegger, 2022). Even the very small marine cyclopoid copepod *O. davisae* shows a jump frequency of 1.6 Hz in large aquaria (Svetlichny et al., 2016). The calanoid copepod *Acartia tonsa* mainly moves by hopping and its jump frequency reaches 2.1 Hz (Decker et al., 2004), whereas the closely related *Acartia clausi* jumps at 1.4 Hz (Saiz and Alcaraz, 1992) and 1.3 Hz (Svetlichny et al., 2017). Thus, large cyclopoid copepods, especially during the brooding state, must maintain a very high jumping frequency to stay in the water column. It remains an open question at which body size threshold copepods, which do not have hydrodynamic and hydrostatic adaptations that reduce their passive descent, change from a planktonic to a benthic life style.

Escape reaction

The escape jumps of NEC females of *M. leuckarti* and *M. albidus* differed from routine jumps not only by their greater speed, but also by a greater ventral oscillation of the body axis during the return phase of the locomotor cycle (Figs 3c and 6). This type of movement is more pronounced in cyclopoids than in calanoids, probably because of the greater propulsive role of the abdomen (Svetlichny et al., 2022). However, in EC females of *M. leuckarti* and *M. albidus*, the oscillations of the body axis were less

than in NEC females during escape swimming. Specifically, the ovisac of EC females was pressed more to the abdomen during escape swimming than during routine jumps, and consequently the shape of their body resembled an articulated ellipsoid. The minimum, average and maximum speeds during the stroke phase of escape jumps in NEC females were significantly higher than those in EC females (Table I) even though EC females pressed their egg sacs to the body during movement. For the larger NEC females of *M. albidus* (total length 0.18 cm), the average speed (31.6 $cm s^{-1}$) and the jump distance (0.36 cm) of the escape reaction was 25% larger than that of smaller *M. leuckarti* (total length 0.15 cm), 35% larger than that of smaller *T. oithonoides* (total length 0.1 cm) and 60% larger than that of the even smaller *O. davisae* (total length 0.05 cm) (Svetlichny et al., 2022) at the same water temperature. This indicates a relationship between movement parameters of escape swimming and body size.

Energy cost of EC

It seems logical that EC females must expend more energy than NEC females to maintain the same level of routine and escape activity. However, the few studies considering the cost of egg transport in planktonic organisms provide contrasting results. EC females of *Neolovenula alluaudi* (Diaptomidae) have a higher oxygen consumption rate than NEC females but the specific oxygen consumption of EC and NEC females was not statistically significantly different (Parra et al., 2003). For *Daphnia magna*, the cost of carrying a brood was negligible (Glazier, 1991). In comparison to NEC females of the calanoid copepods *C. aquaedulcis* and *A. salinus*, EC females had a higher respiration rate by 32.7 and 25.7%, respectively, related to the extra energy expenditures to overcome egg sac gravity and hydrodynamic resistance (Svetlichny et al., 2012b). EC females of the marine calanoid *P. elongatus* carry about 10 eggs per sac (~20% of the body volume), and their expenditure of respiratory energy linked to dragging the egg sac equals to 17% of the energy metabolism of NEC females (Svetlichny et al., 2017). Here, the total mechanical energy of cruising jumps in EC females of *M. leuckarti* was 1.5 times greater than that in NEC females, whereas in *M. albidus*, the difference in the amount of energy spent on small jumps was only 6% because of the lower swimming speed of EC females compared with NEC females (Table II). Considering the same average speeds of routine jumps of *M. albidus*, the power of EC females was 1.5 times greater than that of NEC females. Interestingly, in EC females of both species, the relative energy expenditure to overcome hydrodynamic resistance (69 and 55% of the total in *M. leuckarti* and *M. albidus*, respectively) was greater than that to overcome body acceleration. The cost of transport by routine jumps, calculated as the ratio of energy expended for movement to body weight and distance traveled, was 1.4 and 1.7 times higher for EC females than for NEC females of *M. leuckarti* and *M. albidus*, respectively. Furthermore, the difference in the energy costs to compensate passive sinking in water was even higher. To keep their position in the water column, EC females of *M. leuckarti* and *M. albidus* expended 2.2 and 2.3 times more energy than NEC females, which amounted to 40–60% of the total energy expended during swimming. In comparison, holoplanktonic calanoid copepods need only 14% of the available mechanical energy of swimming to maintain

their position in the water column (Svetlichny *et al.*, 2022). Also, the total mechanical energy spent on jumping during the escape reaction was 16 and 24% greater in EC females than in NEC females of both studied species. The energy required to overcome drag in both species (60–80% of total) was 1.5–4 times greater than the cost of accelerating the body, because of their ability to maintain the kinetic movement energy throughout the escape reaction. The power of escape jumps of NEC females of *M. leuckarti* and *M. albidus* generally corresponded to the average power of jumps of other copepods with similar body sizes (Svetlichny *et al.*, 2020). Similarly, the average mass-specific power of NEC females escape jumps of *M. leuckarti* and *M. albidus* (58–83-W kg⁻¹ body mass) was close to the mass-specific power of escape jumps of *O. davisae*, *A. tonsa* and *Calanus finmarchicus* (Kjørboe *et al.*, 2010a). However, the average mass-specific power of escape jumps of NEC females of *M. leuckarti* and *M. albidus* was 7–10 times less than the record high mass-specific power of hyponeustonic copepods that are capable to jump out of the water during an escape reaction (Svetlichny *et al.*, 2018). The mean costs of transport for the NEC females of *M. leuckarti* and *M. albidus* during the escape response (57.5 * 10⁻³ and 47.3 * 10⁻³ cal g⁻¹ m⁻¹, respectively) were 18 and 33% less than for the EC females and, in general, are close to the cost of transport during the escape reaction in other cyclopoid copepods (Morris *et al.*, 1990).

CONCLUSION

The kinematic parameters of routine jumps (duration, distance and speed) were not related to the reproductive status of female *M. leuckarti* and *M. albidus*. However, the additional load from the egg sacs required a significant increase in power to overcome drag and accelerate the body, and therefore the cost of transport in cruise locomotion of EC females of *M. leuckarti* and *M. albidus* was 28 and 40%, respectively, more than that of NEC females moving at similar speeds. However, the difference in energy costs for maintaining the position in the water column was the most pronounced. Egg sacs doubled the energy necessary to compensate the gravitational descent with respect to NEC females. These expenditures were most critical in EC females of *M. albidus*, which, to be constantly in the water column, had to expend more than half of the energy than they expended during cruising.

During the escape reaction, the average parameters of the entire jump were not clearly related to the reproductive status of females. However, the average and maximum speeds during the stroke phase of a jump were significantly lower by 12–14% in EC females. On the contrary, the power and cost of transport in *M. leuckarti* and *M. albidus* EC females were 16 and 23%, respectively, higher than in NEC females. Thus, if brooding females could make the same escape jumps as non-brooding females, the cost of egg transport during the escape reaction would be even greater. However, such an increase in mechanical power would require additional energy for muscle contraction. The fact that EC females are usually more preyed by predators than NEC ones (Logerwell and Ohman, 1999) indicates their inability to increase the power of movement to compensate for the decrease in the speed of the escape reaction.

SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

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DATA AVAILABILITY

The data sets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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