

RESEARCH ARTICLE

Swim and fly: escape strategy in neustonic and planktonic copepods

Leonid Svetlichny^{1,*}, Poul S. Larsen² and Thomas Kiørboe³**ABSTRACT**

Copepods can respond to predators by powerful escape jumps that in some surface-dwelling forms may propel the copepod out of the water. We studied the kinematics and energetics of submerged and out-of-water jumps of two neustonic pontellid copepods, *Anomalocera patersoni* and *Pontella mediterranea*, and one pelagic calanoid copepod, *Calanus helgolandicus* (*euxinus*). We show that jumping out of the water does not happen just by inertia gained during the copepod's acceleration underwater, but also requires the force generated by the thoracic limbs when breaking through the water's surface to overcome surface tension, drag and gravity. The timing of this appears to be necessary for success. At the moment of breaking the water interface, the instantaneous velocity of the two pontellids reached 125 cm s^{-1} , while their maximum underwater speed (115 cm s^{-1}) was close to that of similarly sized *C. helgolandicus* (106 cm s^{-1}). The average specific power produced by the two pontellids during out-of-water jumps ($1700\text{--}3300 \text{ W kg}^{-1}$ muscle mass) was close to that during submerged jumps ($900\text{--}1600 \text{ W kg}^{-1}$ muscle mass) and, in turn, similar to that produced during submerged jumps of *C. helgolandicus* (1300 W kg^{-1} muscle mass). The pontellids may shake off water adhering to their body by repeated strokes of the limbs during flight, which leads to a slight acceleration in the air. Our observations suggest that out-of-water jumps of pontellids are not dependent on any exceptional ability to perform this behavior but have the same energetic cost and are based on the same kinematic patterns and contractive capabilities of muscles as those of copepods swimming submerged.

KEY WORDS: Copepoda, Escape velocity, Acceleration, Muscle power, Out-of-water jumps

INTRODUCTION

The powerful escape jumps of planktonic copepods are a typical reaction to the threat of a predator (Fields and Yen, 1997), and the accelerations and speeds attained are impressive: speeds exceeding 500 body lengths s^{-1} may be achieved within a few milliseconds (Buskey et al., 2002). These high speeds are accomplished by the sequential beating of the four or five pairs of thoracic swimming legs in metachronal waves, which produces an exceptionally high

force during the power stroke, and mass-specific forces are much higher than the highest forces reported for other organisms (Kiørboe et al., 2010). The ability of copepods to perceive their predators at distance and escape at these exceptional speeds has been cited as key to the evolutionary success of copepods (Kiørboe, 2013), arguably the most abundant metazoans in the ocean (Humes, 1994).

While escape jumps typically occur beneath the surface of the ocean, some surface-dwelling (neustonic) copepods may in fact jump out of the water during escapes. Such aerial jumps were first observed by Ostroumoff (1894) and Lowndes (1935) and described in some detail by Zaitsev (1971), who reported jumps reaching heights of 15 cm and lengths of $15\text{--}20 \text{ cm}$ in 3 mm -sized *Pontella mediterranea*. Out-of-water jumps have the advantage over submerged jumps that they may allow much longer escape distances and bring the copepod beyond the visual range of an attacking fish (Gemmell et al., 2012). However, to become airborne, the copepod has to overcome drag and surface tension, which requires a much larger power than necessary for larger organisms jumping out of the water, such as flying fish. Using high-speed video recordings at $250\text{--}500 \text{ frames s}^{-1}$, Gemmell et al. (2012) reported detailed data on the kinematics of such jumps by the neustonic pontellid copepods *Anomalocera ornata* and *Labidocera aestiva* and provided an analysis of their energetics. Gemmell et al. (2012) arrived at the fundamentally important conclusions that pontellids jump out of the water and overcome the surface tension as a result of the kinetic energy gained when accelerating below the water surface and that the underwater velocity (and therefore energy expenditure) of pontellid copepods is higher than the maximum velocities reported for other similarly sized copepods. They also suggested that 'pontellids may have special adaptations to make it easier for them to jump out of the water', such as a body surface 'that is less wettable than other copepods' and the possibility that 'the copepods inject chemicals during breaking of the surface' to reduce the surface tension.

Planktonic calanoid copepods that live well beneath the surface of the ocean are, however, also able to jump out of the water in artificial laboratory situations, e.g. when placed in a drop of water on the microscope slide, as noted by Lowndes (1935) and observed multiple times by us, suggesting that no special adaptations are required to perform this behavior. Here, we hypothesized that out-of-water jumps of neustonic copepods are made as a result of the same mechanism and the same muscular efforts and energy possessed by similarly sized planktonic copepods jumping submerged in the water. We use high-speed video filming for a comparative analysis of the kinematics and energetics of escape jumps in two neustonic copepods, *Pontella mediterranea* and *Anomalocera patersoni*, jumping both underwater and out of the water, as well as the kinematics of the submerged avoidance response in a pelagic copepod, *Calanus helgolandicus* (*euxinus*). We show that submerged jump speeds, propulsive forces and power expenditure are similar between similarly sized copepods, irrespective of their habitat and taxonomic affiliation, and that no

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particular adaptations are required for neustonic copepods to jump out of the water.

MATERIALS AND METHODS

Laboratory experiments

Copepods were collected in the Black Sea, 2 miles off Sevastopol Bay during the morning between late spring–early autumn 2011–2014. *Anomalocera patersoni* Templeton 1837 and *Pontella mediterranea* (Claus 1863) were collected in the surface layer with a 300 μm mesh size hyponeustonic net, and *Calanus helgolandicus* (Claus 1863) were collected with a 200 μm Nansen net hauled vertically from a depth of 40–60 m. Within 0.5 h, 20–30 individuals were transferred via a wide-mouthed pipette into 200 ml beakers filled with filtered seawater, salinity 18 psu and 25°C. For observations, 1–3 individuals were placed in a small glass cuvette filled with filtered seawater (0.22 μm pore size). We used a small cuvette (1.5 cm height, 3 cm width and 3 cm length) to study out-of-water jumps and a larger cuvette (4×6×1.5 cm³) to study submerged swimming. In the former, the camera was positioned so that the free water surface was in the middle of the field of view in order to capture both the water and aerial phases of an escape response. In the latter, the camera captured the water phase.

A high-speed camera (Nikon 1V1, 1.2 firmware version) equipped with an extension sliding piece for macro photography with 100 mm lens (Industar 100 U; field of view either 2.5×1 cm² or 5×2 cm²) was used to capture the escape behavior. A collimated beam of light from a 10 W LED lamp pointed towards the camera was used to illuminate the cuvette. Escape jumps were recorded at 1200 frames s⁻¹. To stimulate the escape reaction, copepods were exposed to electrical impulses with a frequency of 2 Hz, a pulse width of 5 ms and current density of 0.05 A cm⁻² established between silver electrodes located along the cuvette edges (see

Svetlichny, 1987). After each period of stimulation, the copepods were replaced with new animals. Video sequences showing specimens moving in the focal plane were selected for frame-by-frame analysis. We digitized the geometric center of the prosome of the copepod in each frame and computed velocities and accelerations; accelerations were obtained by numerical differentiation of velocity records. We analyzed eight out-of-water jumps of *P. mediterranea* and one of *A. patersoni*, in addition to 21 and 19, respectively, of submerged jumps as well as 15 submerged jumps of *C. helgolandicus* (Table 1). Morphometric measurements were taken on 20 individuals of each species (Table 1). Body surface area (A_s) was estimated using the equation for the ellipsoid with the longitudinal axis equal to the distance from the end of the head to the end of the genital segment, and the transverse axis equal to maximum body width (D) measured dorsally. Body frontal area (A_f), was calculated as $A_f=0.25\pi D^2$. Body volume (V) was calculated according to Svetlichny et al. (2012) and body mass (M) was calculated as $M=V\rho$, where ρ is body density, taken to be 1.05 g cm⁻³.

We estimated the mass of longitudinal and dorsolateral muscles of the thorax as 27% of the body mass as estimated for *C. helgolandicus* (Svetlichny, 1988). The values presented in the tables and figures are means±s.d.

Data analysis

The video sequences provide the change of position Δs of the geometric center of the prosome during the time step Δt , hence the velocity $U=\Delta s/\Delta t$ and acceleration $\Delta U/\Delta t$. For submerged motion, the added (virtual) mass should be included, but for a prolate ellipsoid approximation of the copepods studied of aspect ratio $L/D\approx 3$ the added-mass coefficient is less than 0.1 (Vogel, 1994, fig. 16.1 therein) and, hence, was ignored. This is in accordance with the experimental result of Svetlichny (1992), who showed that the

Table 1. Body morphology, speed (U) and distance (s) of submerged and out-of-water jumps for the three study species

	<i>Pontella mediterranea</i>	<i>Anomalocera patersoni</i>	<i>Calanus helgolandicus</i>
n , number of observations	20	20	20
L_t , total length (mm)	2.68±0.32	3.43±0.12	3.38±0.17
L , prosome length (mm)	2.02±0.24	2.54±0.16	2.63±0.13
D , prosome diameter (mm)	0.73±0.05	0.88±0.06	0.85±0.04
A_s , body surface area (mm ²)	4.5±0.9	6.3±0.7	6.4±0.6
A_f , body frontal area (mm ²)	0.42±0.06	0.61±0.08	0.57±0.07
V , body volume (mm ³)	0.61±0.14	1.16±0.15	0.93±0.1
M , body mass (g)	6.3×10 ⁻⁴	1.2×10 ⁻³	9.6×10 ⁻⁴
Submerged jumps			
n , number of observations	21	19	15
U_{max} , maximum velocity (cm s ⁻¹)	82.0±17.9	89.8±17.9	92.4±9.1
U_{mean} , mean velocity, in stroke (cm s ⁻¹)	61.4±15.3	65.4±14.2	68.9±11.9
U_{mean} of all jumps (cm s ⁻¹)	48.3±11.3	58.5±13.8	58.1±10.9
Stroke phase duration (ms)	4.9±0.7	5.5±0.9	6.4±1.1
Total duration of kick (ms)	10.4±1.6	9.4±1.5	11.6±1.5
s , distance, stroke phase (cm)	0.31±0.09	0.37±0.11	0.44±0.078
s total kick (cm)	0.50±0.12	0.55±0.11	0.67±0.108
Out-of-water jumps			
n , number of observations	8	1	
U before surface film (cm s ⁻¹)	90.4±20.4	56.2	
U_{max} in film (cm s ⁻¹)	101.06±11.9	121.8	
U detachment from film (cm s ⁻¹)	45.9±7.0	51.5	
U_{mean} after water breaking (cm s ⁻¹)	43.05±5.7	42.5±5.6	
U after ejecting drop (cm s ⁻¹)	46.0±7.3		
Stroke phase duration (ms)	6.7±0.9	4.9	
Duration until U_{max} (ms)	3.45±0.7	1.7	
Time to penetrate surface (ms)	5.5±0.4	4.9	
Total duration of kick (ms)	9.7±1.4		
Duration of jump during flight (ms)	10.2±0.9		

hydrodynamic resistance of *C. helgolandicus* with its antennae pressed to the body is similar in a uniform flow of water and at an accelerated motion with the same instantaneous velocity. Added mass effects are probably important in mechanistic models and analyses of beating appendages (e.g. Morris et al. 1985, 1990; or Jiang and Kjørboe, 2011) but in the present phenomenological interpretation of experimental data from video records, such effects do not appear significant.

The equation of motion is then:

$$MdU/dt = F_p - F_d, \quad (1)$$

where M denotes body mass, F_p is propulsive force and F_d is the drag force when submerged. Gravity and buoyancy forces cancel and we ignore other forces such as of the so-called Basset history term. For non-propulsive deceleration, Eqn 1 provides an estimate of the drag force as a function of velocity, $F_d(U) = -MdU/dt$, and using this relationship for propulsive acceleration in Eqn 1 provides an estimate of the propulsive force F_p . We used periods of uninterrupted, non-propulsive, submerged decelerations to estimate drag force as a function of velocity, which was then used during events of uninterrupted accelerations to estimate propulsive force F_p from Eqn 1.

Alternatively, the drag force can be calculated from:

$$\begin{aligned} F_d &= C_d S^{1/2} \rho U^2; \\ C_d &= C_d(Re); \\ Re &= UD/\nu, \end{aligned} \quad (2)$$

where S denotes the surface area of the prosome, D is its diameter, ρ is density and ν is kinematic viscosity of seawater, and C_d is the Reynolds number-dependent drag coefficient. C_d has been determined experimentally for copepods, including the three species considered here (Fig. 1, based on data from Kurbatov and Svetlichny, 1981; Stepanov and Svetlichny, 1981; Svetlichny, 1983).

Given F_d , the mass-specific propulsive forces can be estimated from F_p/M , and F_p/M_{muscle} , and mass-specific propulsive powers

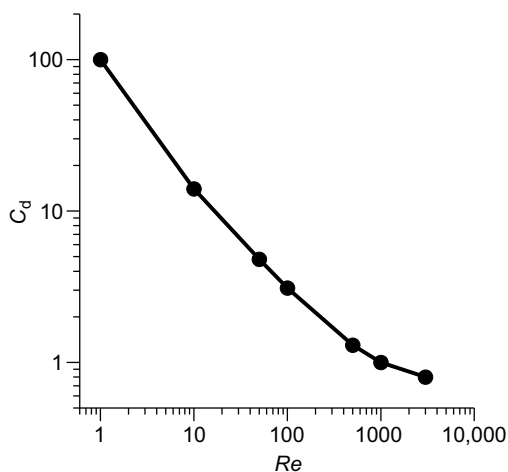


Fig. 1. Drag coefficient (C_d) versus Reynolds number (Re). $Re < 40$: measured on immobilized copepods of the genera *Calanus*, *Pseudocalanus* and *Centropages* sinking in water with the head down and antennules folded along the body (Svetlichny, 1983). Increased body weight was obtained by placing microparticles of lead in the mouth of the copepods. $1 < Re < 3000$: enlarged model of the same copepods sinking in the same manner in glycerol solutions (Kurbatov and Svetlichny, 1981; Stepanov and Svetlichny, 1981).

from:

$$\begin{aligned} P_m &= F_p U / M; \\ P_{\text{muscle}} &= F_p U / M_{\text{muscle}}, \end{aligned} \quad (3)$$

where M_{muscle} denotes the total mass of longitudinal and transverse muscles of the thorax associated with the action of the swimming legs.

We also wanted to estimate the energy expended by a copepod to jump out of the water and become airborne, say from the submerged state a to state b, c or d (see Fig. 4, inset) (see also Gemmell et al., 2012). In state b, one half of the prosome is above the free surface level, in c, all of the prosome is just above the surface level, while in d, the copepod is airborne as the liquid filament snaps. The energy needed is provided by a certain loss of the copepod's kinetic energy plus its work by propulsive kicks during the escape. From a physical point of view, this energy, W_{esc} , is the sum of work done to overcome (i) the resistance due to surface tension, (ii) the drag during motion through water (ignoring that through air as being negligible), and (iii) the increase in potential energy by gaining height when out of the water where buoyancy no longer compensates for gravity.

Multiplying Eqn 1 by U gives the mechanical energy balance. Integrated from the fully submerged state a to, for example, the fully airborne state d over time Δt_{a-d} corresponding to the displacement $\Delta s_{a-d} = U \times \Delta t_{a-d}$, this gives $\frac{1}{2}M(U_d^2 - U_a^2) = \Sigma(F \times \Delta s)_{a-d}$, where the right-hand side is the sum of work done by the acting forces, i.e. power strokes, surface tension, drag and gravity. This equation may be rearranged to:

$$\frac{1}{2}M(U_a^2 - U_d^2) + W_{\text{kick}} = \sigma_s(A_d - A_a) + \frac{1}{2}LF_d + LMg. \quad (4)$$

The left-hand side of Eqn 4 is the energy expended by a copepod. The right-hand side may be called the escape work, W_{esc} , which is the work to be overcome by the copepod in order to become airborne. The first term in Eqn 4, the change (loss) in kinetic energy, is readily obtained from the mass M and velocities derived from video records. The second term, the work done by a propulsive kick, can be estimated from a similar energy balance now applied to a fully submerged acceleration as the sum of change in kinetic energy and work by the drag force, F_d , say from state 1 to 2:

$$W_{\text{kick}} = \frac{1}{2}M(U_2^2 - U_1^2) + \int_1^2 F_d U dt, \quad (5)$$

where F_d depends on U according to Eqn 2 and velocity versus time is obtained from video records of underwater accelerations. In practice, kicks are often overlapping, leading to considerable uncertainty. The right-hand side of Eqn 4 has three contributions: (i) the contribution to resistance due to surface tension is calculated as the work needed to create a new, stretched free surface, $\sigma_s(A_d - A_a)$, where σ_s denotes the air–water surface tension; (ii) the contribution due to submerged drag is based on the mean velocity over a distance of one-half the length L of the prosome; and (iii) the increase in potential energy is calculated as the lifting of the center of gravity a distance of the prosome length L above the free surface, where g denotes the acceleration of gravity.

To illustrate the calculation of the contribution (i) from surface tension we consider the change from a to b because observations (see Results) show that there is often a significant dip in velocity when the copepod reaches position b, after which the velocity increases again due to a new stroke of the limbs. At stage b, one half of the vertical prosome ($\frac{1}{2}L$) is above the free surface level. Based on single frames of the video records showing a variety of shapes of

the deformed surface contour $z(r)$, it is approximated by that generated by rotating a half period of a cosine about the axis of the prosome, leading to the equation:

$$z(r) = 1/4 \times L \times [1 + \cos(\pi r/R)], \quad (6)$$

where z denotes vertical height, r radial distance, L length of the prosome ($=2.02$ mm for *P. mediterranea*) and R the radius to the outer point of the deformed surface, observed to be typically of the order of the diameter of the prosome ($=0.73$ mm). The area of the axisymmetric surface given by Eqn 6 is:

$$A_b = \int_0^R 2\pi r \left[1 + \left\{ \pi L / (4R) \times \sin(\pi r/R) \right\}^2 \right]^{1/2} dr, \quad (7)$$

while the corresponding initial area of the un-deformed surface is:

$$A_a = \pi R^2. \quad (8)$$

An expression similar to Eqn 7 has been derived for the lifted cusp at state d to which we added the surface area of the prosome assumed to have been covered by a liquid film due to the dynamics of the process (see Discussion).

RESULTS

Submerged jumps

Submerged jumps of all three species were rather similar. Individuals respond to electrical stimulations by a series of kicks with the swimming legs giving rise to rapid escape jumps. Each kick-cycle consisted of sequential power strokes of the four or five pairs of swimming legs, and subsequent simultaneous recovery stroke of all legs. The antennules were folded backwards at the first stroke. In the pontellids, the fifth pair of swimming legs was not involved. The jumps could be directed upwards towards the surface, leading to occasional out-of-water jumps, or followed various submerged paths. Typical records of the fluctuating velocity versus time for the three species during submerged jumps consisting of a series of consecutive kick cycles are shown in Fig. 2. Note that in *Calanus helgolandicus*, strokes of the five pairs of thoracic swimming legs may partially act together and the joint action of legs 4 and 5 and of legs 1–3 produces bimodal force impulses and double peaks in velocity. Peak velocity, stroke duration, acceleration and other kinematic characteristics were strikingly similar between the three species (Tables 1 and 2). The large values of standard deviations of results in Table 2 are indicative of natural variation between individual events observed and are probably not exceeded by the uncertainties associated with model assumptions.

We used the decelerations of coasting phases between power strokes for the three species to estimate the species-specific velocity-dependent drag forces from Eqn 1, and compared these with estimates based on the empirical C_d versus Re relationship in Fig. 1 and Eqn 2 (Fig. 3). These two independent estimates of the drag forces were of a similar order of magnitude, which is encouraging. The estimates based on Eqn 1 were rather variable, and so we favored the (slightly smaller) estimate based on the empirical drag coefficient. The velocity range was about 0.1 – 1.0 ms^{-1} for most data of the present study, corresponding to $Re \approx 70$ – 900 where $C_d \approx Re^{-0.5}$ according to Fig. 1, hence $F_d \approx U^{1.5}$ as seen in Fig. 3.

With the estimate of drag and observed accelerations, we computed propulsive forces and specific power output of the submerged escapes for the three species (Table 2). Again, they were rather similar between species. The largest species, *A. patersoni*, produced the largest propulsion force during escape, about 2.5 times

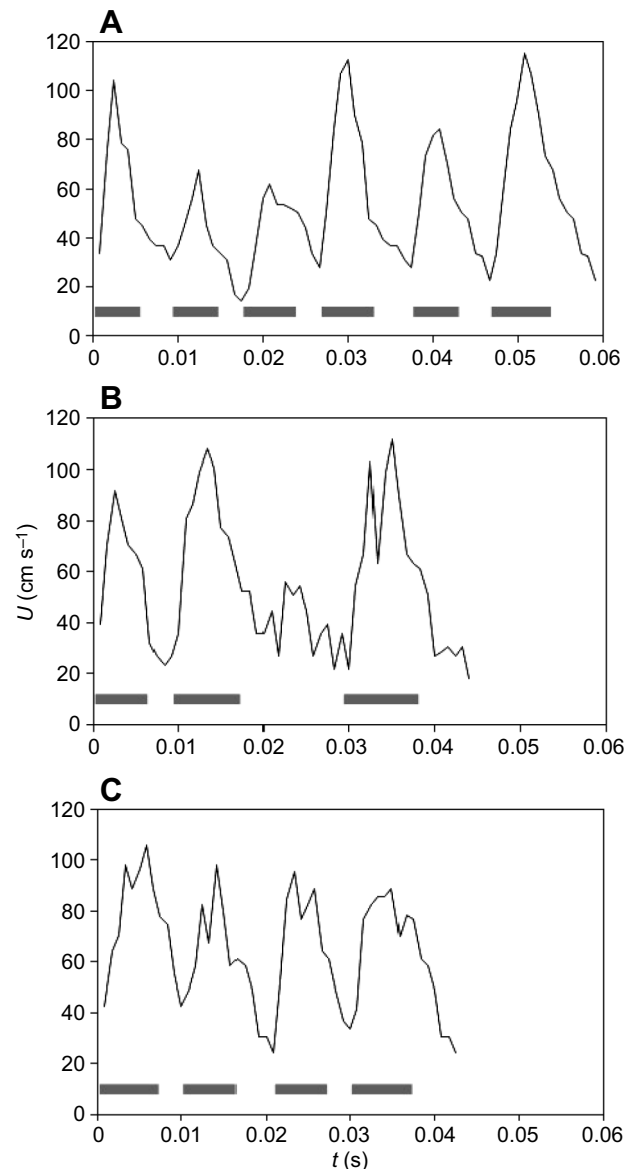


Fig. 2. Instantaneous speed (U) during submerged horizontal escape swimming. Gray rectangles mark stroke phases. (A) *Pontella mediterranea*, (B) *Anomalocera patersoni* and (C) *Calanus helgolandicus*. t is time.

higher than that of the smaller *P. mediterranea*. This difference was reduced when comparing mass-specific power production, with the performance of the pelagic *C. helgolandicus* being between that of the two neustonic species.

Finally, we estimated the magnitude of W_{kick} from Eqn 5 applied to periods of observed accelerations in Fig. 2A–C and Fig. 4 using the velocity-dependent drag F_d from correlations shown in Fig. 3 (Fig. 5). W_{kick} increased linearly with velocity for all three species and the data clearly show *A. patersoni* to be most powerful, followed by *C. helgolandicus* and *P. mediterranea*.

Out-of-water jumps

The spectacular out-of-water jumps in *P. mediterranea* are illustrated in Movie 1. The analysis of eight out-of-water jumps to airborne flight in *P. mediterranea*, as well as some unsuccessful jumps with the animal not leaving the water, showed that success

Table 2. Number of observations, maximal and mean±s.d. values of acceleration, drag force F_d , propulsive force F_p and mass-specific powers for submerged and out-of-water jumps for the three study species

	<i>Pontella mediterranea</i>	<i>Anomalocera patersoni</i>	<i>Calanus helgolandicus</i>
Submerged jumps			
n , number of observations	8	4	5
dU/dt , acceleration ($m\ s^{-2}$)	405, 212±121	540, 443±72	419, 353±50
F_d , drag force (U in $m\ s^{-1}$) (μN)	$247U^{1.45}$	$328U^{1.52}$	$309U^{1.51}$
F_p , propulsive force (μN)	395, 250±104	794, 724±102	556, 500±72
$F_{p,body\ mass}$, body mass-specific force ($N\ kg^{-1}$)	627, 398±166	661, 603±85	564, 521±75
$F_{p,muscle\ mass}$, muscle mass-specific force ($N\ kg^{-1}$)	2324, 1472±614	2449, 2235±315	2090, 1928±276
P_m , mass-specific power ($W\ kg^{-1}$)	611, 252±177	545, 426±129	487, 341±121
P_{muscle} , muscle mass-specific power ($W\ kg^{-1}$)	2020, 932±696	2020, 1579±477	1805, 1263±447
Out-of-water jumps			
n , number of observations	8	1	
dU/dt , acceleration ($m\ s^{-2}$)	389±180	787	
$F_{p,body\ mass}$, body mass-specific force ($N\ kg^{-1}$)	637±158	1015	
$F_{p,muscle\ mass}$, muscle mass-specific force ($N\ kg^{-1}$)	2358±586	3761	
P_m , mass-specific power ($W\ kg^{-1}$)	459±165	903	
P_{muscle} , muscle mass-specific power ($W\ kg^{-1}$)	1701±612	3345	

Drag force (F_d) data are from Fig. 3, propulsive force (F_p) data are from Eqn 1, mass-specific powers (P_m and P_{muscle}) are from Eqns 2 and 3.

occurs only when the beginning of a kick immediately precedes contact of the top part of the body with the water surface. This is illustrated in Fig. 4, which shows body velocity versus time during three kicks of which the first is completely underwater. During the second kick, the copepod jumps out of the water and with the third kick it is completely airborne. The second kick starts with strokes of the fourth and third swimming leg that accelerate the body towards the surface. As the copepod penetrates the surface (stage b in inset of Fig. 4), the speed drops and then increases again with the strokes of the third (p3) and second (p2) pairs of legs (to stage c in Fig. 4), to finally decline again as the body is raised above the water at its full length and airborne flight is achieved. The third kick cycle in the air yields another slight increase in velocity due to ejection of an adhering water drop. Two other sequences showing the variation of velocity during out-of-water jumps and airborne flight are shown in Fig. 6A,B, confirming the dip in velocity as the free surface is penetrated. We managed to record only one out-of-water jump of *A. patersoni*. The female made a jump from a horizontal position, immediately below the surface film and from almost zero speed of the body. A kick from the limbs made it move up through the surface and away with complete detachment from the surface, an event captured in 6 frames (~5 ms) (Fig. 7). Note that we observed no dip in velocity as the surface was penetrated because accelerated movement out of water in *A. patersoni* begins directly from the surface. This is because *A. patersoni* has special hairs on the dorsal side of the body that keep it directly in contact with the surface of the water. Photos of such hairs and a discussion of their role in *A. patersoni* are given by Ianora et al. (1992).

Average kinematics of all eight cases of *P. mediterranea* analyzed plus the one case for *A. patersoni* demonstrate similar stroke kinematics and velocity variation (Figs 5 and 6) and that the appendage kinematics does not differ markedly from the kinematics of submerged jumps (Table 1). Successful out-of-water jumps showed on average higher accelerations and specific power production than submerged jumps within the same species (Table 2). The dip in velocity during penetration of the water surface was observed in five out of eight cases in *P. mediterranea* and corresponds to the loss of kinetic energy. We use the data of Fig. 4 to illustrate the calculations. The dip in velocity after contact with the surface (from $U_a=108\ cm\ s^{-1}$ to $U_b=77\ cm\ s^{-1}$) for a mass of $M=0.63\ mg$ corresponds to a loss of kinetic energy of $0.18\ \mu J$ (or

48%) according to Eqn 4 applied from stage a to b of Fig. 4 (inset). Contributions to the energy expenditure W_{esc} comprise three components: (i) the increase of surface energy, which according to Eqns 7 and 8 for $L=2\ mm$, $R=0.73\ mm$ and $\sigma_s=0.075\ N\ m^{-1}$ becomes $\sigma_s(A_b-A_a)=0.075\times(2.86-1.67)\times 10^{-6}=0.0886\times 10^{-6}\ J=0.09\ \mu J$; (ii) the drag estimated by using the mean velocity from a to b in Eqn 2, $\frac{1}{2}LF_d=0.22\ \mu J$; and (iii) the potential energy $1/4\times LMg=0.003\ \mu J$. The three terms add up to $W_{esc}=0.31\ \mu J$ which is $0.14\ \mu J$ greater than the loss of kinetic energy ($0.18\ \mu J$). This difference in energy is provided by a small part of the two kicks p3 and p2 shown in Fig. 4 to occur during the event. At a velocity of the order of $90\ cm\ s^{-1}$, a kick lasting a full video frame ($1/1200\ s$) would contribute an energy addition of $0.25\ \mu J$ according to Fig. 5, which is more than needed ($0.14\ \mu J$). Including similar calculations for four other cases of observed velocity dip when *P. mediterranea* starts the out-of-water jump, we found the average of five events to involve a reduction of kinetic energy (mean±s.d.) of $0.17\pm 0.08\ \mu J$ while the energy expenditure added up to $W_{esc}=0.27\pm 0.05\ \mu J$, leaving a difference of $0.11\ \mu J$.

We also considered two cases of out-of-water jumps from the time the copepod arrives at the surface until it is fully airborne, state a to d (Fig. 4, inset). First, for *Pontella mediterranea* (Fig. 4) the loss of kinetic energy is estimated to $0.25\ \mu J$ while the three contributions to energy expenditure ($0.40, 0.22, 0.013\ \mu J$) add to $W_{esc}=0.63\ \mu J$, the difference of $0.38\ \mu J$ being ascribed to part of kick p3 plus kicks p2 and p1 lasting about four frames (Fig. 4). But according to Fig. 5 at a copepod velocity of the order of $60\ cm\ s^{-1}$ one kick for the duration of one video frame would provide the additional energy of $0.14\ \mu J$. Second, for *Anomalocera patersoni* (Fig. 7) the loss of kinetic energy was estimated to $0.70\ \mu J$ while the three contributions to energy expenditure ($0.53, 0.76, 0.03\ \mu J$) add to $W_{esc}=1.3\ \mu J$, a difference of $0.62\ \mu J$. This escape lasted about 4 video frames but it was not possible to establish kicks, yet according to Fig. 5 at a velocity of the order of $90\ cm\ s^{-1}$ one kick for the duration of one video frame would provide the additional energy of about $0.4\ \mu J$.

From these examples, it can be seen that the energy expenditure required to overcome drag contributes about 2/3 of the total work, breaking of the water surface tension about 1/3, while the cost of increase in potential energy only contributes ~2% of the total.

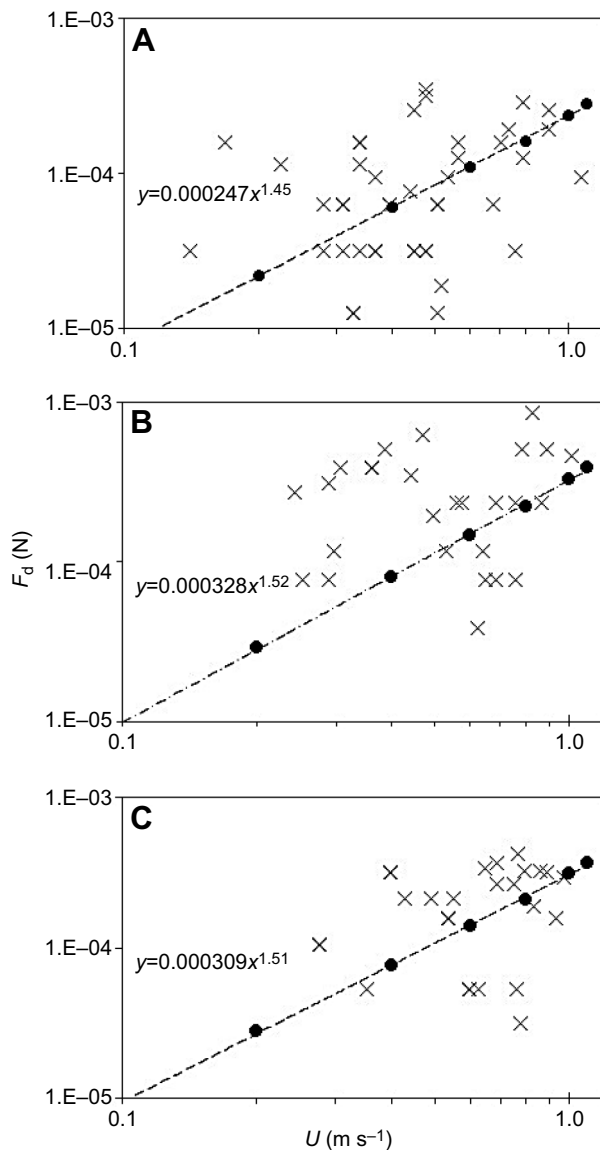


Fig. 3. Drag force (F_d) versus velocity (U). Predictions from observed coasting decelerations and Eqn 1 (crosses) and from empirical C_d versus Re of Fig. 1 (circles) with the regression equation given. (A) *Pontella mediterranea*, (B) *Anomalocera patersoni* and (C) *Calanus helgolandicus*.

DISCUSSION

Kinematics and energetics

The kinematics of copepod escape reactions have been described by many researchers based on high-speed filming of free-swimming individuals (Strickler, 1975; Svetlichny, 1986; Morris et al., 1990; Kiørboe et al., 2010) and of attached individuals (Svetlichny, 1987; Alcaraz and Strickler, 1988; Lenz and Hartline, 1999; Lenz et al., 2004). The escape reaction exhibited by copepods is realized mostly due to metachronal power strokes of the swimming limbs. It has long been realized that the specific muscle force required for the high accelerations and velocities achieved during such jumps is high, and much higher – by an order of magnitude or more – than recorded for startle responses in any other organisms, including flying insects and escaping fish (Marden, 2005). The resulting specific power production is also high and appears to outperform other invertebrates and is similar to or higher than that observed in the most powerful

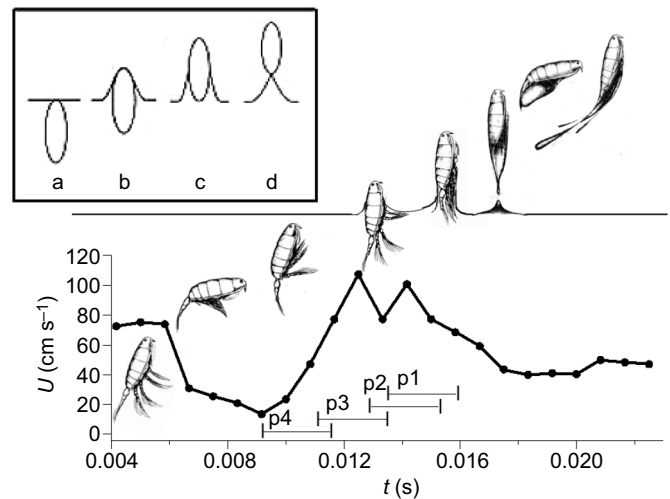


Fig. 4. Velocity of vertical motion during an escape event terminated with an out-of-water jump for *P. mediterranea*. The position of body and limbs of the crustacean are shown by images synchronized with the time scale. Time bars p4 to p1 mark the metachronal strokes of four pairs of thoracic legs. During the second kick (p3), the body approaches and penetrates the free surface, while kicks p2 and p1 lead to an airborne escape. Inset shows stages a, b, c and d during an out-of-water jump (schematic).

vertebrates (Josephson, 1985; Askew and Marsh, 2002). Thus, the power output integrated over one complete jump beat cycle measured in copepods tethered to a force sensor yields estimates of 300–1000 W kg⁻¹ muscle mass in *C. helgolandicus*, *Calanus finmarchicus* and *Undinula vulgaris* (Svetlichny, 1988; Lenz and Hartline, 1999; Lenz et al., 2004), similar to that calculated for free-jumping *C. finmarchicus* (300 W kg⁻¹; Kiørboe et al., 2010). The mean values reported here for both *C. helgolandicus* and the two pontellids are somewhat higher (approximately 1000–3300 W kg⁻¹ of muscles; Table 2). The advantage of the present estimates is (i) that they are based on free-swimming rather than tethered copepods that may have a 50% slower power stroke (Svetlichny, 1987), and (ii) that the calculations are based on drag that agrees with values inferred from observed coasting decelerations rather than based on idealized drag laws. At any rate, it is the unusual force and power production that

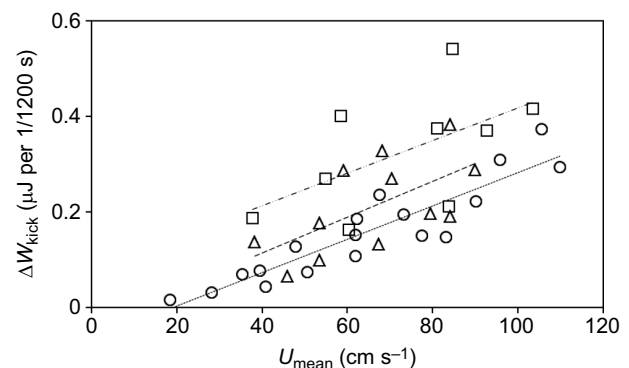


Fig. 5. Contribution of kick energy (W_{kick}) during submerged acceleration in one 1/1200 s period of video record versus mean velocity during the period. Lines are linear regressions of kick energy (y) versus mean velocity (x) and are $y=0.003x+0.077$ ($R^2=0.32$) for *A. patersoni* (squares), $y=0.004x-0.034$ ($R^2=0.39$) for *C. helgolandicus* (triangles), and $y=0.004x-0.067$ ($R^2=0.84$) for *P. mediterranea* (circles).

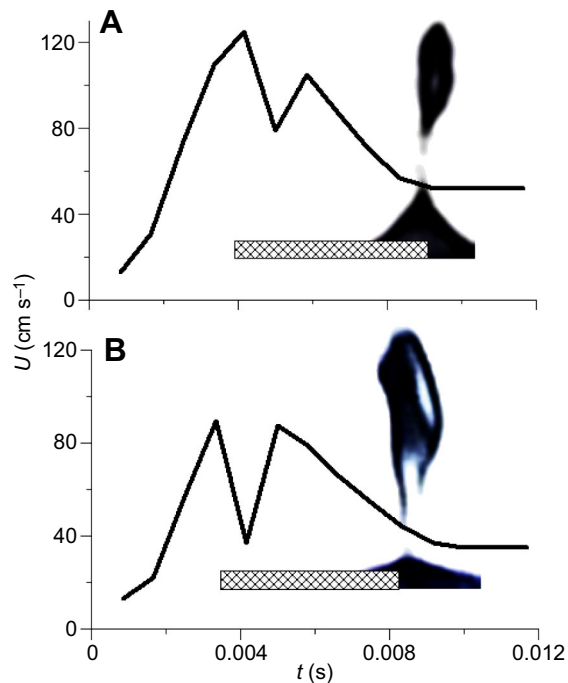


Fig. 6. Velocity of vertical motion during an out-of-water jump resulting in a velocity dip in *P. mediterranea*. Two examples of copepod separation from the surface film are shown in A and B, where B illustrates how a large drop of water (visible white) can adhere to the body. Rectangles indicate the period when the crustacean broke through the surface film of the water.

allows these small animals to rather easily break the surface tension and overcome liquid drag, provided the timing of kicks is right. Such capabilities are otherwise normally ascribed to larger organisms, like fish, where the energy required to break the surface tension is low relative to that required to overcome drag and gravity.

The resistance to escape from surface tension was based on the work done to stretch the free surface from a given initial area to a larger area when the copepod rapidly emerged above the water level. Single frames from the video records clearly showed that liquid surrounding the prosome was lifted and at no point revealed a dry prosome surface with a point of contact indicating a contact angle. The stretched water–air surface appeared smooth. These observations lead us to propose the surface form of Eqn 5 for state b and that of state d as the sum of the raised cusp plus a film covering the prosome. The key is the rapid dynamics of the process and the

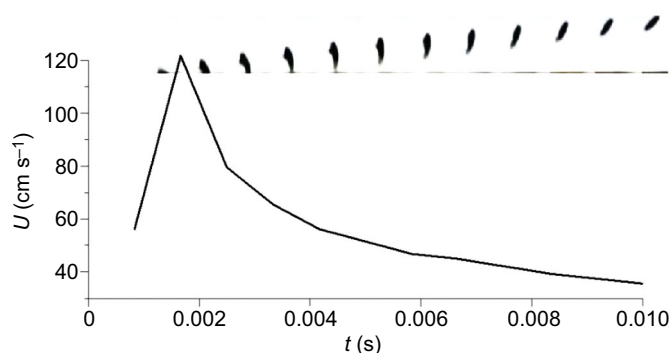


Fig. 7. Instantaneous speed during an out-of-water jump for *A. patersoni*. Data are shown with a synchronized storyboard.

associated hysteresis effects of wetting and de-wetting of solid surfaces (de Gennes, 1985). This model of the physics is quite different from that of Gemmell et al. (2012), who determined the energy loss as the change in surface energy of static states from when the prosome surface area A was fully in contact with water to fully in contact with air. They then used Young's law to obtain their eqn 2.4, $\text{loss} = \sigma_s A \cos\theta$, where the contact angle θ was measured from video records. Gemmell et al. (2012) also state 'in order to maintain a useful level of kinetic energy after breaking the surface the copepod body surface has to be hydrophobic, i.e. much larger contact angle in the 68–81 deg range'. As θ approaches 90 deg, this loss becomes zero, so it may have a questionable contribution to the energy changes, particularly because its validity is based on static states.

Our estimates of energy cost of penetrating the free surface (to explain either the velocity dip of Fig. 4 or the full escape to become airborne) exceed the corresponding loss of kinetic energy by amounts that are of the order of 0.11–0.14 μJ and 0.38–0.62 μJ , respectively. We ascribe these amounts to additional contributions from propulsive kicks that may last one or two frames of video record, and depending on velocity, the magnitude may be judged from the estimates shown in Fig. 5. Although this only provides a qualitative explanation, the main conclusion is that *P. mediterranea* needs $W_{\text{esc}} = 0.63 \mu\text{J}$ to become airborne and *A. patersoni* needs $W_{\text{esc}} = 1.3 \mu\text{J}$ for the cases analyzed, and that these amounts are not provided by the observed losses of kinetic energy alone. In fact, we can calculate the minimal initial velocity required to become airborne, i.e. $U_{\text{min}} = U_a$, $U_d = 0$ in Eqn 4 and ignoring W_{esc} , as $U_{\text{min}} = (2 \times W_{\text{esc}} / M)^{1/2} = (2 \times 0.63 / 0.63)^{1/2} = 1.42 \text{ m s}^{-1}$ and $U_{\text{min}} = (2 \times 1.32 / 1.2)^{1/2} = 1.49 \text{ m s}^{-1}$, respectively, for the two cases. Such high values of velocity have not been observed.

Gemmell et al. (2012) estimated that $\sim 2/3$ of the kinetic energy loss at the moment when the copepod starts to break the water surface is due to the penetration of the surface, but only $\sim 1/3$ if integrated over the entire phase, from state a to d. Our estimates show that observed loss of kinetic energy is insufficient to overcome the resistance from surface tension and submerged drag, and that escape requires well-timed propulsive kicks when breaking through the water surface. This has been established as a result of a finer temporal resolution of the observations (250–500 Hz versus 1200 Hz). Taken together, these observations suggest that relative to the power production of these copepods during out-of-water jumps, overcoming the surface tension is a significant yet affordable cost.

The large variation of the values in Table 2 partly reflects natural variations between analyzed events. Thus, the relative contribution to propulsive acceleration and drag varies significantly among events: drag contributes from 23% to 67% for the eight out-of-water jumps of *P. mediterranea* mainly because a given magnitude of acceleration may occur at relatively low or high velocity, and drag increases with velocity to the power of about 1.5 (Fig. 3). While accelerations are well estimated, excessive drag may therefore lead to an overestimation of propulsive force and specific power. The heights and lengths of airborne jumps of several tenths of a centimeter in copepods reported by early observers (cited in the Introduction) appear unrealistic as they are much greater than the 4 cm heights and 8 cm lengths of jumps observed by us and by Gemmell et al. (2012) and would require initial airborne velocities of $\sim 2 \text{ m s}^{-1}$ or more, much higher than any observations reported later.

Different or similar?

Are neustonic copepods that routinely do out-of-water jumps more powerful than copepods that live far from the surface? Our data

suggests that the specific force and power production vary between the three species, yet are rather similar, and the submerged *C. helgolandicus* is in all respects intermediate between the two neustonic species (Table 2). That being said, within species, acceleration, propulsive force and mass-specific power are about 1.6–2.1 times larger on average for out-of-water jumps than for submerged jumps. While the values for the former are still within the range of observed values for the latter, this does suggest that it is only the most powerful jumps that bring the copepods into the air. Also, the analysis of unsuccessful out-of-water jumps of *A. patersoni* and *P. mediterranea* indicates that stroke phase synchronization when approaching the water surface is crucial to overcome surface tension and gravity forces successfully. In this regard, the sensory system of pontellids, unique among copepods, including numerous eyes placed on both dorsal and ventral surfaces of the head, may play a key role.

Gemmell et al. (2012) suggested that pontellids jumping out of the water may have a less wettable surface than mesopelagic species. However, pontellids can carry water droplets adhering to their body as they jump out of the water, according to our estimates amounting to about 1/4 of the body weight for *P. mediterranea*. Such observations suggest that neustonic copepods, leaping into the air to escape fish predators, have not acquired any adaptations to reduce the wetting properties or drag force of their body. The maximum instantaneous velocities registered in *P. mediterranea* and *A. patersoni* at the moment they overcome the surface film (125 and 122 cm s⁻¹, respectively) are faster than the maximum speed of underwater swimming of the two species and of *C. helgolandicus* (106 cm s⁻¹). However, these peak speeds happened when the top part of the pontellids' body was in the air already while the thoracic limbs made strokes in the water (Fig. 4).

Finally, our conclusion that out-of-water jumps in copepods require no particular adaptations is supported by the fact that copepods normally living far from the surface of the ocean in artificial situations can likewise jump out of the water, as reported for calanoid copepods (Lowndes, 1935; Tanaka, 2014). The physical model with spherical particles shooting towards the liquid surface to mimic planktonic copepods jumping (Kim et al., 2015) cannot fully simulate an out-of-water jump of a copepod but similarly suggests 'that it is unlikely that aerial jumping of copepods requires special adaptations to their body surface properties in order to make it easier for them to jump out of the water'.

Kim et al. (2015) argued that small copepods like *Acartia tonsa* cannot jump out of the water because they are not capable of generating a high enough speed of the body before reaching the free surface, according to the kinetic energy concept of Gemmell et al. (2012). However, *A. patersoni* makes a jump into the air directly from a still position and from the surface film to which it is attached by dorsal setae. According to the concept and analysis developed here, the success and speed of the flight depends only on the speed and force of the limbs and abdomen. Although propulsive force and counteracting surface tension can both be proportional to the square of the linear dimensions of the body, the ability of copepods to jump out of the water can be limited by the insufficient step length of legs and the usual jump distance of small copepods. The success of jumping out of the water still depends on the ability to create a well-timed propulsive force by the limbs.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.S., T.K.; Methodology: L.S., P.S.L.; Validation: P.S.L.; Formal analysis: L.S., P.S.L., T.K.; Investigation: L.S.; Writing - original draft: L.S., P.S.L., T.K.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.167262.supplemental>

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