

# Optimal swimming strategies in mate-searching pelagic copepods

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**Abstract** Male copepods must swim to find females, but swimming increases the risk of meeting predators and is expensive in terms of energy expenditure. Here I address the trade-offs between gains and risks and the question of how much and how fast to swim using simple models that optimise the number of lifetime mate encounters. Radically different swimming strategies are predicted for different feeding behaviours, and these predictions are tested experimentally using representative species. In general, male swimming speeds and the difference in swimming speeds between the genders are predicted and observed to increase with increasing conflict between mate searching and feeding. It is high in ambush feeders, where searching (swimming) and feeding are mutually exclusive and low in species, where the matured males do not feed at all. Ambush feeding males alternate between stationary ambush feeding and rapid search swimming. Swimming speed and the fraction of time spent searching increase with food availability, as predicted. This response is different from the pattern in other feeding types. The swimming speeds of non-feeding males are predicted and observed to be independent of the magnitude of their energy storage and to scale with the square root of body length in contrast to the proportionality scaling in feeding copepods. Suspension feeding males may search and feed at the same time, but feeding is more efficient when hovering than when cruising. Therefore, females should mainly be hovering and males cruising, which is confirmed by observations. Differences in

swimming behaviour between genders and feeding types imply different mortality rates and predict well the observed patterns in population sex ratios. Sex ratios may become so female-biased that male abundances limit population growth, demonstrating that behaviours that are optimal to the individual may be suboptimal to the population.

**Keywords** Cost of swimming · Feeding behaviour · Population dynamics · Sex ratio · Sexual selection · Trade-offs

## Introduction

Planktonic organisms move to find food and mates, to avoid predators and to remain suspended. However, moving comes at a price, both in terms of the metabolic expenses associated with moving and as an increased risk of the likelihood of meeting predators. Consequently, trade-offs have to be made. Motility behaviour varies greatly between species, both in terms of swimming patterns and swimming speeds (Mauchline 1998; Johansen et al. 2002; Visser and Kiørboe 2006), and these differences may to a large extent be interpreted as adaptations to optimise the trade-offs between gains and risks, with different best strategies in different environments or contexts. Among plankton, one classical example is diurnal vertical migration in zooplankters that may vary with the absence or presence of predators (Bollens and Frost 1989; Frost and Bollens 1992; Loose and Dawidowicz 1994; Van Gool and Ringelberg 1998). Motility behaviour may also depend on the availability of food, an example of which is that swimming speed typically increases and motility becomes more directionally persistent in the absence of food (Fenchel and Jonsson 1988; Menden-Deuer and Grünbaum

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2006; Van Duren and Videler 1995; Tiselius 1992). This behaviour enhances the chance of finding food but also that of meeting predators, but the optimum motility behaviour may change towards a more risky one with increasing need of finding food (Kerfoot 1978; Mengl and Orsi 1991).

Optimisation studies of motility patterns and flight or swimming speeds in aerial and aquatic organisms have mainly focussed on energetic constraints (e.g. foraging gains vs. cost of transport; Hedenström and Ålerstam 1993, 1996; Ruxton and Bailey 2005; Behrens et al. 2006) or examined motility strategies that balance the need to avoid predators and maximise food intake (Titelman and Fiksen 2004; Visser and Kiørboe 2006). In this study I examine how sexual selection determines copepod motility behaviour by considering the fundamental undertakings of feeding, predator avoidance and reproduction simultaneously. I chose the simple system of pelagic male copepods searching for females and attempt to define the male swimming speed that maximises its fitness, quantified as the expected number of lifetime mate encounters.

Among pelagic copepods it is the male which typically performs active mate searching. This is a strong indication of sperm competition and of a non-limiting supply of sperm (Kokko and Wong 2007). The typical mate-finding pattern is that the female signals her presence and position by means of chemical cues, while the male searches for cues and females (Mauchline 1998; Yen et al. 1998; Tsuda and Miller 1998), much the same way as has long been known for many insects (Bossert and Wilson 1963; Nesbitt et al. 1973). Because the extension of the female pheromone signal and, therefore, mate encounter rate is largely independent of the motility of the female (Bagøien and Kiørboe 2005a), but directly proportional to male swimming speed, male copepods typically move more, faster and with higher directional persistence than the females (Kiørboe and Bagøien 2005). Consequently, males run elevated risks of meeting predators, with the implication that male mortalities may be higher than female mortalities, similar to what has been described for many insect systems, particularly moths (Acharya 1995; Svensson 1996). This may explain why sex ratios in adult field populations often are very female-biased (Kiørboe 2006) and suggests that there is strong selective pressure on swimming speeds in general, with sexual selection, in particular, governing male speeds.

In pelagic copepods, swimming may interfere with feeding, and differences in feeding strategies may therefore imply different optimal swimming strategies. Among males there are basically three feeding strategies – no feeding upon maturation, ambush feeding and suspension feeding. Ambush feeding copepods remain almost stationary in the water or sink very slowly while waiting for potential prey to pass by. For ambush feeders, there is therefore a strong

conflict between feeding (no swimming) and mate searching (no feeding). Suspension feeders generate a feeding current by beating their appendages. As this current may also drive the copepod through the water, suspension feeders may feed and search for females simultaneously. However, feeding becomes more efficient – by about 50% – if the copepod is “hovering”, i.e. oriented such that the feeding current balances gravity and the copepod is almost stationary in the water (Strickler 1982; Tiselius and Jonsson 1990; Christensen-Dalsgaard and Fenchel 2003). Thus, again there is a conflict between feeding and searching, but it is not as pronounced for the suspension feeder as for the ambush feeder because a cruising male suspension feeder may feed, albeit at a lower than maximum rate. In non-feeding males there is, of course, no conflict. The different intensities of conflicts between feeding and mate searching may lead to different optimal mate searching strategies.

In this report I first present simple models for the three different feeding strategies that optimise the trade-offs between female encounters on the one hand and predator risk and metabolic expenses of swimming on the other in terms of average number of mates met in a lifetime. Model predictions are subsequently tested against observations of swimming speed and pattern in three species, each representing one of the three different feeding strategies: *Pseudocalanus elongatus* (non-feeding males), *Oithona davisae* (males ambush feeding) and *Temora longicornis* (suspension feeding).

## Methods

Experimental animals were reared in the laboratory at approximately 16°C (*T. longicornis*, *P. elongatus*) or 22°C (*O. davisae*), and all experiments were conducted at these temperatures. For measurements of swimming speeds, recently matured males or females were picked from the culture (in case of *O. davisae* the sexes were separated before maturation). Between 15 and 25 copepods were placed in an aquarium and allowed at least 1 h for acclimation in the dark before filming was initiated. A small aquarium (8 × 8 × 8 cm<sup>3</sup>) was used for the tiny *O. davisae* (cephalothorax length 0.3 mm) and a larger one (10 × 10 × 10 cm<sup>3</sup>) for the other, larger species (approx. 1 mm). At these densities encounters between individual copepods were rare, and swimming behaviours thus likely unaffected by density. The aquarium was illuminated from the back by light from an infrared diode that was collimated through a condenser lens, and the copepods were video-recorded from the front by a B/W CCD camera equipped with a 35-mm objective. Three- to six-minute sequences were stored on a computer, and two-dimensional projections of swimming tracks were later digitised using

LABTRACK (Bioras, Kvistgård, Denmark). All individuals within the field of view were included, and at least 100 tracks were analysed for each species and treatment, unless otherwise stated. Estimates of swimming speeds were computed from position differences between consecutive video frames (25 Hz); in this way ten thousands of individual speed measurements were obtained for each species. Frequencies of swimming speeds and average swimming speeds were computed from these observations, and no attempts were made to separate the observations between individuals. For the two feeding species, the males were either fed flagellates (*Rhodomonas salina* for *T. longicornis* or *Oxhyrris marina* for *O. davisae*) ad libitum or starved during the recording as well as during the preceding 24 h. Females of *P. elongatus* were similarly fed *R. salina*.

Additional motility observations were made on *O. davisae* males at a range of defined food concentrations, with *O. marina* offered as food at concentrations of 0, 10, 100 or 1000 cells ml<sup>-1</sup> during the video-recording and during the preceding 24 h. During the acclimation period, the copepods were incubated with food in 0.5-l bottles mounted on a slowly rotating plankton wheel to keep the food suspended and homogeneously distributed.

Another experiment examined the age variation in adult male *P. elongatus* swimming speeds. Age was used as a proxy for the amount of body reserves left in the non-feeding males of this species. About 25 recently (1–4 days) matured males were added to the observation aquarium where they were maintained in darkness for more than 3 weeks and their swimming behaviour video-recorded almost daily.

In addition to swimming observations on the main target species, I also quantified swimming in two other species (*Temora stylifera*, *Acartia granii*, both at 22°C) using a similar approach. *Temora stylifera* is a suspension feeder; *A. granii* probably feeds similarly to other *Acartia* species, with feeding bouts alternating with sinking (Tiselius and Jonsson 1990). These species were also taken from laboratory cultures.

The theoretical observations below suggest that the optimal swimming speed in ambush feeding males depend on their feeding rate. Therefore, I measured *O. davisae* male feeding rate as a function of prey concentration in simple incubation experiments. Suspensions of *O. marina* at seven different concentrations between 20 and 600 cells ml<sup>-1</sup> were put into 75-ml NUNC culture bottles, and 20–40 adult males were added to each of these bottles (lowest concentration of animals at lowest concentration of prey). There were two bottles with animals and three controls without animals at each concentration. The bottles were incubated on a slowly rotating wheel for 24 h. Initial and final prey concentrations were quantified in samples taken in the initial suspension and in each bottle at the end of

the incubation period. Cells were counted using the Utermöhl technique. All equations were solved using *Mathematica*.

## Theoretical considerations

### The predation problem

I first consider the predation problem separately as it applies similarly to all the feeding strategies. The fitness of a male copepod is defined as the number of females that he meets in a lifetime,  $N$ . This, in turn, is equal to the female encounter rate ( $E$ ) multiplied by the average male longevity,  $\tau$ . I use simple encounter formulations. Thus, males meet females at rate:

$$E = \pi R_{\text{Female}}^2 v C_{\text{Female}} = K_1 v \quad (1)$$

and predators at a rate,  $m$ :

$$m = \pi R_{\text{Predator}}^2 (u^2 + v^2)^{0.5} C_{\text{Predator}} = K_2 (u^2 + v^2)^{0.5}, \quad (2)$$

where  $R_{\text{Female}}$  and  $R_{\text{Predator}}$  are the distances at which males detect females and predators detect males, respectively,  $v$  and  $u$  are male and predator swimming speeds, respectively, and  $C_{\text{Female}}$  and  $C_{\text{Predator}}$  are the concentrations of females and predators, respectively.  $K_1$  and  $K_2$  are constants. See Table 1 for symbols. The assumption that mate encounter rate is directionally proportional to male swimming speed is warranted by the typically high degree of directional persistence in swimming males (Kiørboe and Bagøien 2005). The predator encounter rate,  $m$ , is also an estimate of the predation mortality. Assuming that predation is the sole source of mortality, the average longevity of an adult male is:

$$\tau = \int_0^T e^{-mt} dt = \frac{1 - e^{-mT}}{m}, \quad (3)$$

where  $T$  is the maximum possible lifespan. If there are no other sources of mortality than predation, we can let  $T$  be infinity, in which case the average longevity equals the inverse of the mortality rate,  $\tau = m^{-1}$ .

We can now compute the average number of female encounters in a lifetime that a male will experience

$$N = E\tau = \frac{E}{m} = \frac{K_1}{K_2} \frac{v}{(u^2 + v^2)^{0.5}}. \quad (4)$$

This function has no optimum but increases monotonically with increasing male swimming speed (Fig. 1a). It implies that if only the predation problem is considered, the optimum swimming behaviour of the male is to swim as fast as possible. This conclusion is independent of the magnitude of all the parameters that go into  $K_1$  and  $K_2$

**Table 1** Definition of symbols used in the equations and the magnitude of the default parameters

Symbol	Explanation	Units	Default parameters	
			<i>Pseudocalanus elongatus</i>	<i>Oithona davisae</i>
$a^a$	½ body width	cm	0.013	0.0063
$N$	Number of lifetime mate encounters	–	–	–
$E$	Female encounter rate	day <sup>-1</sup>	–	–
$m$	Predator encounter rate = predations mortality rate	day <sup>-1</sup>	–	–
$\tau$	Average longevity	day	–	–
$R_{\text{Sex}}$	Mate detection distance	cm	–	–
$R_{\text{Pred}}^b$	Prey detection distance	cm	0.63	0.30
$v$	Male swimming speed	cm s <sup>-1</sup>	–	–
$u^c$	Predator swimming speed	cm s <sup>-1</sup>	2.5	1.2
$K_1$	$\pi R_{\text{Sex}}^2 C_{\text{Female}}$	cm <sup>-1</sup>	–	–
$K_2$	$\pi R_{\text{Pred}}^2 C_{\text{Pred}}$	cm <sup>-1</sup>	$1.25 \times 10^{-3}$	–
$K_3^d$	Finite body reserve of non-feeding male	J	0.038	–
$C_{\text{Fem}}$	Concentration of adult females	cm <sup>-3</sup>	–	–
$C_{\text{Pred}}$	Concentration of predators	cm <sup>-3</sup>	$10^{-5}$	–
$T$	Maximum lifespan	day	15	–
$M^e$	Basal energy expenditure	J s <sup>-1</sup>	$1.7 \times 10^{-8}$	$2.5 \times 10^{-8}$
$\alpha^f$	$=6 \times 10^{-7} \pi \eta a / \text{efficiency of energy-transformation}$	J s cm <sup>-2</sup>	$2.5 \times 10^{-8}$	$1.2 \times 10^{-8}$
$f^g$	Feeding rate	J s <sup>-1</sup>	–	$1.1 \times 10^{-7}$
$q$	Fraction of time spent swimming	–	–	–
$\eta$	Viscosity	g cm <sup>-1</sup> s	$10^{-2}$	$10^{-2}$

<sup>a</sup>  $0.21 \times$  cephalothorax length (Davis and Alatalo 1992)

<sup>b</sup>  $10 \times$  prey length

<sup>c</sup>  $40 \times$  prey body lengths s<sup>-1</sup>

<sup>d</sup> ½ times total body energy content. Body carbon estimated from length-carbon regression (Uye and Matsuda 1988) and body carbon converted to joules assuming  $0.046 \text{ J } (\mu\text{g C})^{-1}$  (Salonen et al. 1976)

<sup>e</sup> Initial estimates of basal metabolism from Ikeda et al. (2001). Oxygen uptake converted to equivalent energy assuming  $0.0221 \text{ J } (\mu\text{l O}_2)^{-1}$ . In *P. elongatus*, basal metabolism was estimated as 0.1 times the estimate from Ikeda et al. (2001) and in *O. davisae* as 0.5 times that estimate. See text for further explanation

<sup>f</sup> Default efficiency of energy transformation is 1%

<sup>g</sup> The maximum feeding rate of male *O. davisae* measured in the present experiments

(reaction distances and concentrations of predators and females).

### The energetics problem

I now include energetic constraints in the considerations and examine the three male feeding strategies separately.

#### Male does not feed

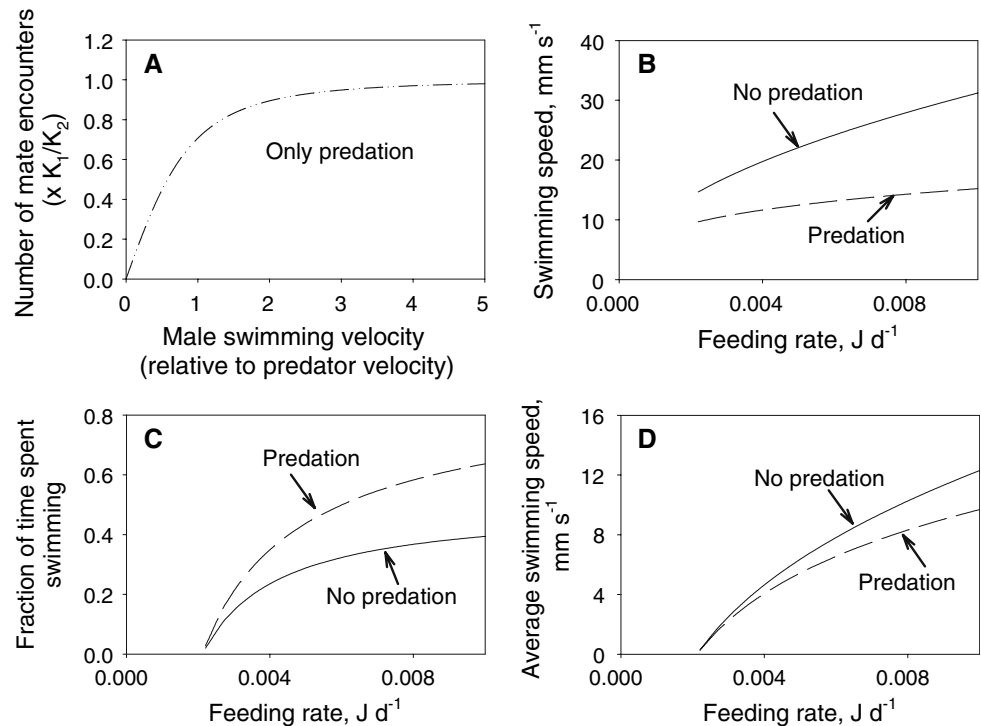
This applies to many copepods among the “higher” calanoid superfamilies (Ohtsuka and Huys 2001) and includes *Pseudocalanus* spp. Assume that the male has a finite resource available for combustion (ultimately limited by

his body mass),  $K_3$ , that he has a constant basal energy expenditure for metabolism ( $M$ ) and that the energy expenditure for swimming increases with swimming speed squared ( $\alpha v^2$ ). The latter is because the drag force at low *Reynolds number* scales with speed (for a sphere), and the power requirement is force times distance per unit time = force  $\times$  speed. The coefficient scales with the body size, the fluid viscosity and the efficiency of energy transformation (Berg 1993; Table 1). The resource has been exhausted after time  $T$ :

$$\frac{K_3}{M + \alpha v^2} = T \quad (5)$$

at which time he will die. The lifetime number of encounters ( $N$ ), if there are no other sources of mortality, is now:

**Fig. 1** **a** Predicted relative number of lifetime mate encounters as a function of male swimming speed, **b** predicted optimal swimming speed, **c** fraction of time spent swimming, **d** average swimming speed as a function of feeding rate in ambush-feeding male copepod in scenarios with and without predation. **b–d** Computed using the default parameters for *Oithona davisae* (Table 1)



$$N = E \cdot T = vK_1T = \frac{K_1K_3v}{M + \alpha v^2} \tag{6}$$

$$\frac{dN}{dv} = 0 \tag{10}$$

We need find the swimming speed that maximises  $N$ , i.e.

$$dN/dv = 0 \Rightarrow v = (M/a)^{0.5} \tag{7}$$

The differential is straightforward but convoluted:

$$\frac{dN}{dv} = \frac{1}{K_2} \left( \frac{(1-A)u^2}{(u^2 + v^2)^{1.5}} + \frac{AK_3v^2K_2(M - \alpha v^2 - 2\alpha u^2)}{(u^2 + v^2)(M + \alpha v^2)^2} \right) = 0 \tag{11}$$

Somewhat surprisingly, the optimum swimming speed is independent of the magnitude of the resource. Because metabolism increases approximately with body mass raised to power 2/3 and, hence, with body length squared (Ikeda et al. 2001), and the  $\alpha$ -coefficient increases approximately with length (compare above), Eq. 7 implies that optimum swimming speeds of non-feeding males should increase with the square root of their body length. This is a testable prediction.

where

$$A = \exp \left( -\frac{K_2K_3(u^2 + v^2)}{(M + \alpha v^2)} \right) \tag{12}$$

The male is also subject to predation mortality (Eq. 2), and the average longevity ( $\tau$ ) of a male subject to this mortality rate and with a maximum lifespan of  $T$  is (combine Eqs. 2, 3, 5):

$$\tau = \frac{1 - \exp(-K_2(u^2 + v^2)^{0.5}(K_3/(M + \alpha v^2)))}{K_2(u^2 + v^2)^{0.5}} \tag{8}$$

In this case, the lifetime female encounters,  $N$ , is:

$$N = vK_1\tau = \frac{K_1v(1 - \exp(-K_2(u^2 + v^2)^{0.5}(K_3/(M + \alpha v^2)))}{K_2(u^2 + v^2)^{0.5}} \tag{9}$$

Unfortunately, there is no analytical solution to Eq. 11, so we must appeal to numerical solutions.

In general, the introduction of predation mortality selects for higher male swimming speed. However, for any realistic combination of parameters (see below), the numerical solution to Eq. 11 is well approximated by the solution without predation (Eq. 7).

*Male is an ambush feeder*

This would apply to, for example, *Oithona davisae*. In this case there is a conflict between feeding and searching. While feeding, the male does not swim; hence he finds no females. While swimming after females, he cannot feed.

Again, we have to find the male swimming speed that yields the highest  $N$ , i.e. solve the equation below for  $v$ :

The male spends energy on two things: basal metabolism ( $M$ ) and swimming. The latter is proportional to the

swimming speed squared ( $v^2$ ), as determined above, as well as to the fraction of time spent swimming ( $q$ ). He gains energy from feeding. Energy acquisition rate is proportional to the feeding rate ( $f$ ) and to the time allocated to feeding, which is  $1 - q$ . The constraint is that energy input has to balance expenditures. Thus:

$$M + \alpha v^2 q - f(1 - q) = 0 \quad (13)$$

where the first term is the basal metabolism, the second term is the energy expenditure for swimming and the third term is the energy gain from feeding. Solving Eq. 13 for  $v$  yields:

$$v = \left( \frac{f(1 - q) - M}{\alpha q} \right)^{1/2}. \quad (14)$$

In the absence of (adaptation to) predation, the male should maximise the *average* swimming speed,  $V = vq$ , as this will optimise the female encounter rate. We find the optimum by putting  $dV/dq = 0$ , which yields

$$q = \frac{f - M}{2f}. \quad (15)$$

Equation 15 implies that the optimum fraction of time spent swimming is independent of the actual cost of swimming. It also implies that the males should swim at most half the time and less if the basal metabolic rate corresponds to a significant fraction of the feeding rate. Combining Eqs. 14 and 15 yields the optimum swimming speed

$$v = \sqrt{\frac{f}{\alpha}}. \quad (16)$$

From Eqs. 15 and 16 it follows that with decreasing food availability (declining  $f$ ), the optimum fraction of time spent swimming and swimming speed (when swimming) both decline (Fig. 1b, c).

Again, we need to worry about the predation mortality. As above, the male needs to optimise total lifetime encounters, which is

$$N = K_1 v q \tau \quad (17)$$

where  $v$  is given by Eq. 15 and  $\tau$  is the inverse of the predation mortality rate (Eq. 2); hence

$$N = \frac{K_1}{K_2} \frac{vq}{(u^2 + v^2)^{0.5}} = \frac{P \left( \frac{f(1-q)-M}{\alpha q} \right)^{1/2}}{\left( u^2 + \frac{f(1-q)-M}{\alpha q} \right)^{1/2}} \times \frac{K_1}{K_2}. \quad (18)$$

We now find the  $q$  that satisfies

$$\frac{dN}{dq} = 0 \quad (19)$$

which yields the optimum fraction of time spent swimming:

$$q = \frac{-(4fM - 4f^2 + \alpha fu^2 - \alpha Mu^2) - (f - M)u\sqrt{\alpha(8f + \alpha u^2)}}{4(f^2 - \alpha fu^2)}. \quad (20)$$

(There are two solutions with the other one being non-physical). Optimum swimming speed still follows from Eq. 14. Predation increases the optimum fraction of time spent swimming and decreases the swimming speed compared to a situation without predation, and both parameters again increase with increasing food availability (Fig. 1b, c). However, predation has only a slight effect on the average swimming speed ( $v \times q$ ) (Fig. 1d). Note that the optimal fraction of time spent swimming (Eq. 20) and the optimal swimming speed (Eq. 14) are both independent of the actual predation pressure (i.e. whether there are many or few predators), with the latter only depending on the predator swimming speed: higher predator speed implies that the male should swim less (lower  $q$ ) but faster (higher  $v$ ).

#### Male is a suspension feeder

Many of the calanoid copepods with feeding adult males (mainly among the lower calanoid super-families; Ohtsuka and Huys 2001) are suspension feeders, and this group includes *Temora* spp. If the feeding current of a suspension feeder is directed horizontally, the copepod will move through the water, while if it is directed downwards, it will be countered by gravity and the copepod will remain stationary in the water (hovering) or move slowly up or down. Because hovering produces a somewhat more efficient feeding current (50%) than cruising but leads to no mate encounters, the prediction is that females should be mainly hovering, while males should be mainly cruising horizontally and moving faster through the water than the females. I refrain from more detailed, quantitative predictions.

#### Predictions

The above theoretical considerations can be summarised in a number of testable predictions:

1. In species with chemical mate signalling, males are expected to swim faster than females because mate encounter rate is proportional to male speed and almost independent of female speed. In species with hydro-mechanical mate-signalling, the roles of the two sexes are almost symmetrical (Bagøien and Kiørboe 2005b), and male and female speeds are expected to be similar.
2. For non-feeding and ambush-feeding males, one may predict the optimum swimming speed based on estimates of basal metabolism, feeding rates and cost of swimming (Eqs. 11, 14, 20).

For males that do not feed, I further predict that:

3. Male swimming speed in inter-species comparisons scales with the square root of body length (Eq. 7), which is potentially different from females, juveniles and males of feeding copepods.
4. Male swimming speed is independent of the magnitude of the energy storage available (Eq. 7). Even though this resource diminishes as the copepod ages, one would therefore expect the optimum swimming speed to remain constant with age.

For ambush-feeding males I predict that

5. Motility alternates between almost stationary ambush feeding and rapid swimming. The fraction of time spent searching (swimming) is predictable from feeding rate, metabolism, cost of swimming and predator swimming speed (Eq. 20).
6. Ambush feeding male swimming speed and fraction of time spent swimming increases with food availability (Fig. 1; Eqs. 14, 20).
7. Male swimming speed is high relative to that of other copepod males. This is most easily seen by comparing non-feeding and ambush feeding males in the absence of predation (Eqs. 7, 16): as long as the feeding rate ( $f$ ) exceeds the basal metabolic rate ( $M$ ), ambush feeding males should swim faster than non-feeding males by a factor of  $(f/M)^{0.5}$ .

For suspension feeding copepods, I predict that

8. Males cruise mainly horizontally at higher speed than females that are mainly hovering

## Results

### Swimming speeds and patterns

Female swimming speeds increased with body size, and relative swimming speeds (body lengths per second) varied

only by a factor of approximately 2. In contrast, male swimming speeds varied independently of size, and relative speeds varied by almost an order of magnitude between species (Table 2).

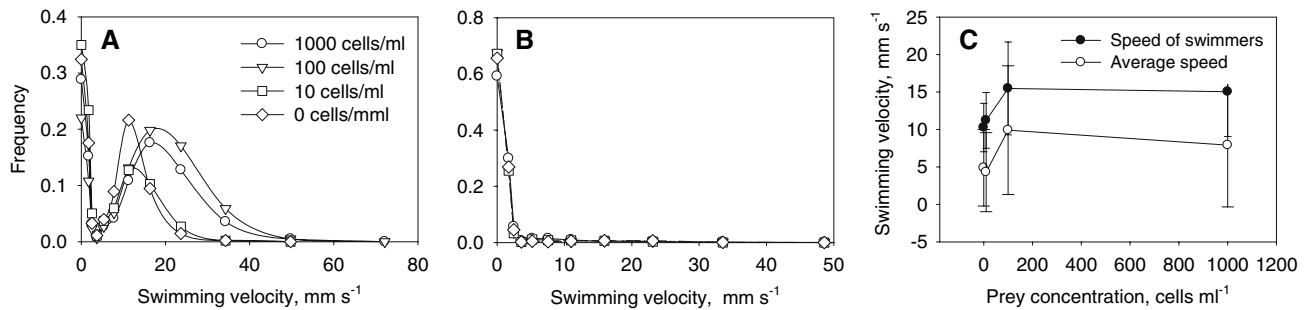
Male swimming speeds and patterns were related to feeding mode. The largest difference in swimming speed between the two sexes was in the ambush feeding *O. davisae*, where average male swimming speed was >15-fold larger than female average move speed. Females feed almost constantly, and feeding implies very slow sinking, only interrupted by 0.5–1 mm long jumps every few seconds, leading to a net move speed of about 0.5 mm s<sup>-1</sup> in the females. Jump speeds are on the order of >20 mm s<sup>-1</sup>, while sinking speeds are 0.2 mm s<sup>-1</sup>. In the frequency distribution of move speeds (Fig. 2a, b), the three lowest bin-classes correspond to feeding individuals. The females feed for more than 95% of the time, independent of food concentration. The males alternate between feeding and swimming at high speed, as is evident from the move speed frequency distribution (Fig. 2a). The swimming speed of swimming individuals depends on the food concentration, apparently in an on/off manner. At low or no food, males were swimming at about 10 mm s<sup>-1</sup> when swimming, increasing to about 15 mm s<sup>-1</sup> at concentrations of prey (*O. marina*) higher than 100 cells ml<sup>-1</sup> (Fig. 2c). Well-fed males ( $\geq 100$  prey cells ml<sup>-1</sup>) also spent a larger fraction of time swimming ( $q = 0.57$ ) than when they were offered no or little food ( $\leq 10$  prey ml<sup>-1</sup>) ( $q = 0.38$ ).

The females of the suspension-feeding copepods (*P. elongatus* and the two *Temora* species) all moved quite slowly since they were mostly hovering. In contrast, the suspension feeding males (the two *Temora* species) moved twice as fast as the females as they were mainly cruising horizontally (Fig. 3). As a result, in both *Temora* species average horizontal speeds in the males were about twice the vertical speeds, while in the females they were similar (Table 3). Swimming speeds of starved males and females *T. longicornis* were identical to those of fed ones (data not shown).

Sex differences in swimming speed were lowest among the last two of the examined species. Non-feeding males of *P. elongatus* only swam slightly faster than the females,

**Table 2** Grand average swimming speeds ( $\pm$ SD) and cephalothorax lengths of males and females of five species of copepods

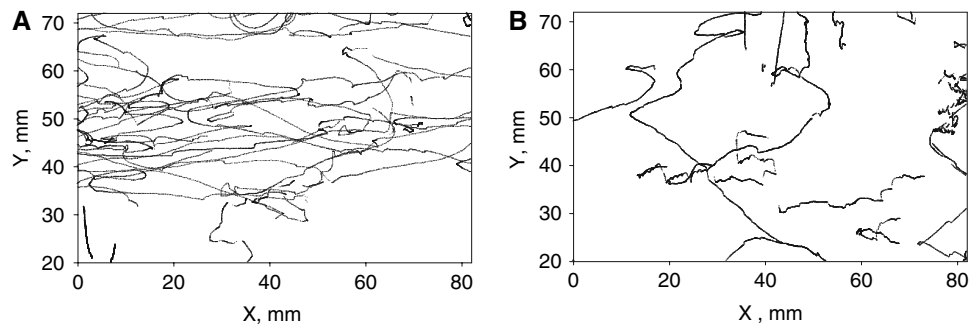
Species	Cephalothorax length (mm)		Swimming speed (mm s <sup>-1</sup> )		Relative swimming speed (body lengths s <sup>-1</sup> )	
	Male	Female	Male	Female	Male	Female
<i>Oithona davisae</i>	0.30	0.34	8.0 $\pm$ 8.2	0.5 $\pm$ 0.6	27	1.5
<i>Acartia granii</i>	0.88	1.01	3.4 $\pm$ 8.4	3.3 $\pm$ 5.0	3.9	3.3
<i>Temora longicornis</i>	0.68	0.74	3.0 $\pm$ 2.3	1.4 $\pm$ 1.9	4.4	1.9
<i>Temora stylifera</i>	0.99	1.07	7.2 $\pm$ 4.6	3.3 $\pm$ 3.5	7.3	3.1
<i>Pseudocalanus elongatus</i>	0.64	0.79	2.8 $\pm$ 3.0	2.0 $\pm$ 2.6	4.4	2.5



**Fig. 2** *Oithona davisae*. Observed frequency distribution of swimming speeds in males (**a**) and females (**b**) at various concentrations of food; **c** average swimming speeds ( $v$ ) of swimming males and overall average swimming speed ( $v \times q$ ) as a function of the concentration of

prey, *Oxhyrris marina*. The trend lines in **b** and **c** are included to help read the graph and should not be interpreted as interpolation curves. Error bars in **c** are standard deviations

**Fig. 3** Two-dimensional projections of swimming tracks of *Temora longicornis* males (**a**) and females (**b**). Each plot represents 20,000 individual position observations, and dots – to the extent visible – are separated by 0.04 s in time



**Table 3** Horizontal ( $V_x$ ) and vertical ( $V_y$ ) average swimming speeds ( $\pm$ SD) in *Temora longicornis* and *Temora stylifera*

Species		$V_x$ (cm s <sup>-1</sup> )	$V_y$ (cm s <sup>-1</sup> )
<i>Temora longicornis</i>	Male	2.4 $\pm$ 2.2	0.9 $\pm$ 1.6
	Female	0.8 $\pm$ 1.5	0.7 $\pm$ 1.4
<i>Temora stylifera</i>	Male	5.4 $\pm$ 5.1	3.5 $\pm$ 4.7
	Female	2.3 $\pm$ 3.5	3.0 $\pm$ 5.2

Vertical and horizontal swimming speeds differ significantly in males ( $P < 5\%$ ) but not in females

while male and female *A. granii* swam at similar speeds. Starving females swam faster ( $2.2 \pm 2.4$  mm s<sup>-1</sup>) than feeding ones, thus making the difference in swimming speed between the sexes even less.

In a separate experiment, the age-variation in swimming speeds of adult male *P. elongatus* was examined (Fig. 4). In these experiments, the average speed was a little lower than that reported above, but the average speed remained constant throughout the 24 days that observations were continued. The number of individual position-observations during 5-min video-clips was fairly constant during the first 10 days, and then declined exponentially. The number of position observations may be considered as a proxy of the survival of these non-feeding males and suggests an average longevity of >13 days and a maximum lifespan of >24 days at 16°C.

#### *Oithona davisae* male feeding rate

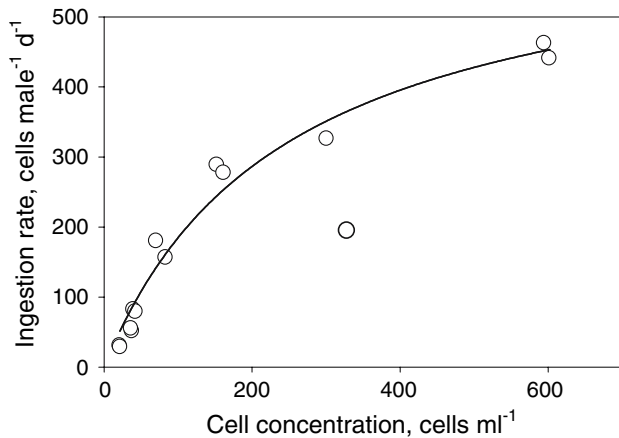
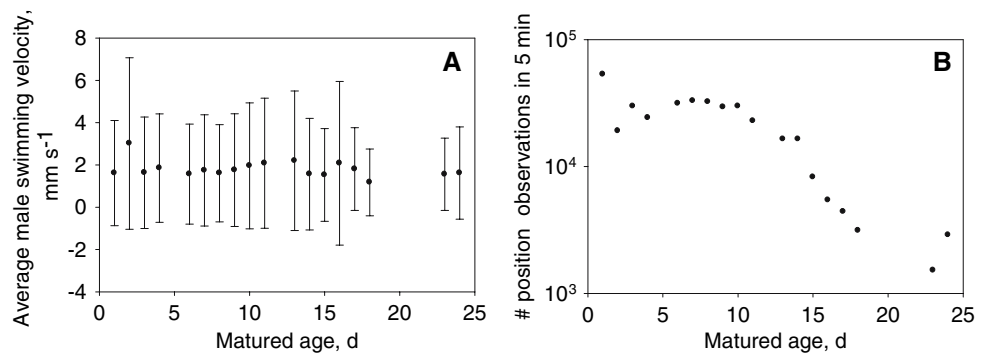
*Oithona davisae* male feeding rate increased with the concentration of prey cells, becoming saturated at prey concentrations exceeding 600 cells ml<sup>-1</sup> (Fig. 5). The functional response in feeding rate to prey concentration was more gradual than the response in swimming speed (Fig. 2). Fitting Hollings disk equation to the observations yields a maximum ingestion rate of 640 cells day<sup>-1</sup>, corresponding to about 0.17  $\mu$ g C day<sup>-1</sup> (*O. marina* carbon content from Saiz et al. 2003) or 0.007 J day<sup>-1</sup> (Table 1).

#### Discussion

Several studies of swimming and flight speeds in aquatic organisms and birds have examined optimal strategies that balance the need to avoid predators and maximise food intake (Tiselius et al. 1997), optimise the trade-off between swimming and feeding (Strathmann and Grünbaum 2006), minimise power requirements for moving, cost of transport during migration (Behrens et al. 2006) or migration time (Hedenström and Ålerstam 1993) or maximise rates of food intake or growth (Ware 1975) or food provision for offspring (Norberg 1981). In many cases these studies have been successful in predicting observed swimming and



**Fig. 4** *Pseudocalanus elongatus* males. Swimming speed ( $\pm$ SD) as a function of age after sexual maturation (a) and total number of digitised copepod positions per 5-min period within a fixed observation volume as a function of matured age (b)



flight speeds. One general result is that optimal move speeds may be highly dependent on the context, and in birds, for example, may vary dramatically between aerial display, migration and foraging (Hedenström and Ålerstam 1996). The inter-specific variation in swimming speeds among male pelagic copepods is high and largely unrelated to body size (Fig. 6a); this is in contrast to swimming speeds of non-male pelagic copepods that increase in proportion to body size (Fig. 6b). I suggest that a significant part of the variation in male swimming speeds can be explained as adaptations to fulfil the male mission of finding as many females as possible during a lifetime. The above models suggest radically different optimum swimming speeds and patterns for different feeding behaviours and lead to a number of testable predictions. In the following I first test each of the eight predictions and subsequently discuss more general aspects of motility strategies and examine population implications of individual swimming behaviours.

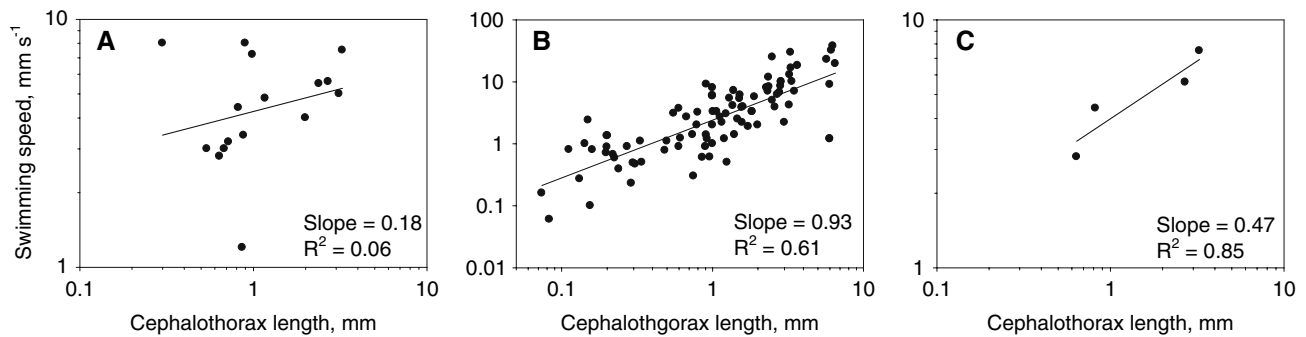
Testing predictions

*Prediction 1: Males swim faster than females in species with chemical mate signalling*

Among the five species examined here, male swimming speeds exceeded female speeds in the four species using chemical signalling in mate finding and were similar among the two sexes in the species using hydromechanical mate signalling (*A. grani*, author's unpublished observation) (Table 2). Additional scattered observations from the literature (Doall et al. 1998; Strickler 1998; Tsuda and Miller 1998 and references in Mauchline 1998; Nihongi et al. 2004; Kiørboe and Bagøien 2005) partly support this: in 13 sets (including the present) of inter-sex comparisons in species with chemical mate signalling, males were swimming faster than females in ten cases; in three sets in species with hydrodynamic signalling, males and females were consistently swimming at similar speeds.

*Prediction 2: Swimming speeds in ambush feeding and non-feeding males are predictable from metabolism, feeding rate and energetic cost of swimming*

While we may estimate the energetic cost of swimming as the power required to overcome friction, the efficiency by which combusted matter is transformed into motion is likely to be low; Berg (1993) states that this is "at most a few percent". Also, there may be a significant loss of energy associated with the movement of appendages (Morris et al. 1985). Measurements and considerations of Svetlichny and Hubareva (2005) suggest a metabolic requirement of 100× the power required to account for frictional losses of body propulsion in a copepod, *Calanus euxinus* – i.e. a gross efficiency of 1%. This includes expenses for moving feeding appendages. They quote their own earlier studies in two other species for gross efficiencies of 0.1 and 0.2%. The study of Buskey (1998) is the only one in which respiration rate has been measured as a function of swimming speed in copepods (*Dioithona*



**Fig. 6** Copepods swimming speeds as a function of size for adult males (a), adult females and juveniles (b) and non-feeding adult males (c). Data include the author's personal observations, data compiled by Mauchline (1998) and Titelman and Kiørboe (2003) as

well as data from Doall et al. (1998), Strickler (1998), Tsuda and Miller (1998), Nihongi et al. (2004) and Kiørboe and Bagøien (2005). Slopes and  $R^2$  values for log–log regression are shown

*oculata*). Fitting his measured respiration rates to a function of the form  $R = M + \alpha v^2$  leads to an estimate of  $\alpha = 0.0178 \text{ J s cm}^{-2}$  and an efficiency of 0.02%, which is very low. Based on this information, I take an efficiency of 1% as a default value but acknowledge that the efficiency of energy conversion and the actual cost of swimming are known only within very large limits.

To predict the magnitude of the optimum swimming speed in non-feeding *P. elongatus* males, I used the default parameter values and conversion factors shown in Table 1. Several of the parameters can be constrained. As a starting point I estimated the basal metabolic rate from the relation of metabolism versus body mass and temperature reported by Ikeda et al. (2001). If the cost of swimming is disregarded and it is assumed that the male will die once half his body mass has been combusted (the males do not have significant lipid resources), then the maximum longevity can be estimated from Eq. 5 to be 2.6 days, which is obviously inconsistent with males surviving for up to about tenfold longer. The basal metabolism is, however, one-tenth of that estimated from Ikeda et al. (2001), and the discrepancy is probably due to the non-feeding status of the males (may account for a factor of four; Kiørboe et al. 1985) and the fact that respiration rates were measured in moving copepods (which may account for a factor of 2–3; Morris et al. 1985).

Assuming a gross efficiency of energy conversion of 1%, the optimum male swimming speed (Eqs. 7 or 11) can be estimated to be  $8.2 \text{ mm s}^{-1}$ , which is substantially higher than that actually observed (Table 2). However, this prediction is not very accurate due to the large uncertainty of the magnitude of the efficiency of energy conversion. If, instead, an efficiency of 0.1% is assumed, which is well within the range of efficiencies considered above, the predicted speed is  $2.6 \text{ mm s}^{-1}$ , which is very similar to that observed. Thus, the observed speed is at least consistent with the theoretical considerations.

Predation only affects the optimum swimming speed in non-feeding males under extreme conditions. Using default

predator parameters (Table 1), identical swimming speeds are predicted with and without predation. One can increase predator reaction distance by one order of magnitude or predator concentration or swimming speed by three orders of magnitude over the default values without significant effects on predicted swimming speed. This, of course, does not mean that predation does not affect male longevity and, consequently, the number of matings in a lifetime; it means that optimal swimming speed is identical whether or not there are predators in the environment.

Using default values for ambush-feeding males of *O. davisae* (Table 1) as well as the measured feeding rates, it is possible to predict swimming speed in scenarios with and without predation (Fig. 1). The observations are consistent with predictions with predation: the predicted swimming speed is  $14.4 \text{ mm s}^{-1}$ , which is similar to that observed ( $15.5 \pm 6.0$  and  $15.1 \pm 6.0$  at the two highest prey concentrations). Observed and predicted overall average swimming speeds ( $v \times q$ ) are also consistent (Fig. 1d vs. Fig. 2c). In the absence of predation, which rarely occurs in nature, males should swim less and faster.

*Prediction 3: In non-feeding males, swimming speed scales with the square root of body length*

The observed square-root scaling in non-feeding males is consistent with the prediction and different from the scaling in feeding copepods, but not significantly so due to the scarcity of data (Fig. 6b, c).

*Prediction 4: In non-feeding males, swimming speed is independent of the magnitude of body reserves*

As the males of non-feeding *P. elongatus* age, their body reserves diminish, but their swimming speed remains constant, as predicted (Fig. 4a).

**Prediction 5:** In ambush feeding males the fraction of time spent swimming is predictable from metabolism, feeding rate, and the energetic cost of swimming

Again using measured feeding rates and default energetic values for ambush feeding males of *O. davisae* (Table 1), well-fed males are predicted to swim 61% of the time ( $q = 0.61$ ), which is similar to that observed ( $q = 0.52$  and  $0.64$  at the two highest prey concentrations, Fig. 2a).

**Prediction 6:** In ambush feeding males, swimming speed and fraction of time spent swimming increase with food availability

*O. davisae* males swim less and slower at low than at high food, as predicted (Fig. 2). Although this may appear intuitive, it is not a trivial result as it differs radically from the response to resources seen in the other species (swimming independent of the resource in *P. elongatus* males, *T. longicornis* males and females or increased speed in the absence of food in *P. elongatus* females)

**Prediction 7:** Ambush feeding males swim faster than other copepods

Ambush feeding *O. davisae* males swim relatively much faster than other copepods (Table 2), and the average relative speed of 27 body lengths  $s^{-1}$  is the highest reported for any copepod to date (data compiled in Fig. 6b). The predicted enhancement in swimming speed of an ambush feeding over that of a non-feeding male is  $(f/M)^{0.5} = (1.1 \times 10^{-7}/0.5 \times 10^{-8})^{0.5}$ , which is approximately sixfold; this is not that different from the observed ratio of relative swimming speeds of *O. davisae* and *P. elongatus*,  $27/4.4 =$  sixfold (using feeding rate of *O. davisae* and the metabolism of a similarly size non-feeding male as computed in Table 1).

**Prediction 8:** Suspension feeding males cruise mainly horizontally and swim faster than the mainly hovering females

Males of both of the two *Temora* species were moving mainly horizontally and faster than the females, which is consistent with the expectation (Fig. 3; Table 3).

Feeding strategy, predation, and the effects of density dependence

The observations are largely consistent with predictions and demonstrate that adaptations to maximise mate

encounters lead to radically different motility behaviours among male copepods depending on their feeding behaviour. Despite the large differences in expected predation mortality, the effect of predation on optimal swimming speed is rather limited: there is no effect on non-feeding males, and only a limited effect on the overall average swimming speed ( $q \times v$ ) in ambush feeding males, indicating that the presence of predators does not lead to an optimal swimming speed that significantly reduces predation risk. In fact, when the energy constraints are disregarded, the prediction is that the males should swim as fast – and risky – as possible. This may be surprising and different from other aspects of plankton motility, where, for example, the vertical migration behaviour is expected to be – and often is – dependent on the presence or absence of predators.

Density dependence of mating systems has recently received considerable interest (Kokko and Rankin 2006), but the present model assumes that optimal male search behaviour is independent of female density. This assumption may be compromised in (at least) two ways. First, if female density becomes so high that mate encounter rate exceeds the mating capacity of the males, then mate encounters are not limiting male reproduction and males should therefore adopt a less risky and more energy-saving motility mode when females are abundant – i.e., swim less and/or slower. It is often assumed that sperm is a non-limiting resource for mating in sexually reproducing animals (see Wedell et al. 2002), and the same assumption has been made here. There is evidence for a variety of organisms, however, that the cost of sperm production is nontrivial (Dewsbury 1982; Van Voorhies 1992; Olsson et al 1997), and this may also apply to copepods. Non-feeding males obviously only have a finite number of spermatophores at their disposal, on the order of 10–100 (Mauchline 1998), and the few available measurements of sperm production rates in feeding males are surprisingly low, one to only a few spermatophores per day (Ianora and Poulet 1993; Kiørboe 2006). Thus, sperm production and mating capacity rather than encounter rates may at times limit mating rate. This situation may apply to small, neritic species, such as *Oithona davisae*, where mate encounter rates during peak season may exceed the males' mating capacity by an order of magnitude or more (Kiørboe 2007). Whether the males' swimming strategy in fact changes with increasing female density or whether it is stereotypic remains to be tested. Second, the availability of receptive females may change over the adult lifespan of a male. Such changes may be of particular relevance to populations with a high degree of synchronisation of maturation among individuals in species where the females can store sperm and, hence, need to be mated only once. In such cases, the source of receptive females in a cohort declines, and there

would thus be a race between males to find virgin females; mate encounter rate will then be more important than total number of mate encounters as a mate encountered late may already be fertilised. This situation would lead to more and/or faster swimming than predicted here. Such a scenario may play a role in copepods in very seasonal environments and with one annual generation (e.g. large copepods of the *Calanus* genus in arctic environments) but be less relevant for the smaller copepods from warmer environments with many overlapping generations considered here. Again, it remains to be examined whether copepods from different environments realise different swimming strategies.

### Population implications

The tailoring of motility behaviour in male copepods to optimise individual reproductive performance has implications for population structure and population processes mediated through effects of motility on mortality. Faster swimming leads to a higher predator encounter rate and, for non-feeding males, also to a shorter maximum lifespan. Differences in swimming speeds between sexes therefore lead to differences in mortality rates and to biased population sex ratios. Observed grand patterns in adult sex ratios in copepod field populations are, in fact, consistent with the differences in motility behaviour reported here. The sex ratio at the time of sex determination has to be near 1:1 (Charnov 1982). If one assumes an equal sex ratio at the time of maturation, then at steady state the adult population sex ratio will equal the ratio of average adult longevity between the sexes. If predation is the only source of mortality, this equals the inverse of the ratio of instantaneous mortality rates of the two genders. Thus, for ambush feeding *O. davisae*, where males swim 15-fold faster than females, one would expect adult male:female sex ratios in field populations of down to 1:15 if all predators were ambush feeders (i.e.  $u = 0$ ); it would be higher if the dominating predators are motile. Very low relative male abundances are, in fact, characteristic for populations of *O. davisae* (seasonal average 0.17; Uye and Sano 1995) and other ambush feeding oithonid copepods (average for the genus: 0.16; Kiørboe 2006). Conversely, one would expect much more equal sex ratios in field populations of *Temora* and *Acartia* spp., where swimming speeds vary by a factor of two or less between genders, which is consistent with average male:female ratios in these families of 0.6–1.0 (Kiørboe 2006). In the case of non-feeding males, the average adult longevity is determined both by the maximum possible life span ( $T$ ) as well as by the instantaneous predation mortality ( $m$ ). Taking *Pseudocalanus* spp. as the example and assuming similar instantaneous mortalities between the genders due to similar swimming speeds, the predicted ratio of male to female

average longevity is  $\frac{1-e^{-mT}}{m} / \frac{1}{m} = 1 - e^{-mT}$  (from Eq. 3). With  $m = 0.045 \text{ days}^{-1}$  (Ohman and Wood 1996) and  $T = 15 \text{ days}$  (Table 1), an intermediate male:female ratio of 0.5 is estimated, which is not too different from the average reported for *Pseudocalanus* spp. field populations (0.27; data compiled by Hirst and Kiørboe 2002).

Low absolute and/or relative abundances of adult males due to behaviour-induced high mortalities may at times constrain the fertilisation rates of females and, hence, lead to less-than maximum population growth rates. Fertilisation limitation has been demonstrated in populations of species with both ambush- and non-feeding males (Hopkins 1982; Kiørboe 2007). The limitation of mating rate due to a shortage of males reinforces Allee-effects (positive density-dependent population growth; Stephens et al. 1999) and restrains the critical minimum population density required for population maintenance (Gerritsen 1980; Kiørboe 2006) in addition to limiting population growth rate. This demonstrates that motility behaviours that are optimal to the individual may be suboptimal to the population.

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### References

- Acharya L (1995) Sex biased predation on moths by insectivorous bats. *Anim Behav* 49:1461–1468
- Bagøien E, Kiørboe T (2005a) Blind dating – mate finding in planktonic copepods. I. Tracking the pheromone trail of *Centropages typicus*. *Mar Ecol Prog Ser* 300:105–115
- Bagøien E, Kiørboe T (2005b) Blind dating – mate finding in planktonic copepods. III. Hydromechanica communication in *Acartia tonsa*. *Mar Ecol Prog Ser* 300:129–133
- Behrens JW, Praebel K, Steffensen JF (2006) Swimming energetics of the Barent Sea Capelin (*Mallotus villosus*) during the spawning migration period. *J Exp Mar Biol Ecol* 331:208–216
- Berg HC (1993) Random walks in biology. Princeton University Press, Princeton
- Bollens SM, Frost BW (1989) Predator-induced diel vertical migration in a planktonic copepod. *J Plankton Res* 11:1047–1065
- Bossert WH, Wilson EO (1963) The analysis of olfactory communication among animals. *J Theor Biol* 5:443–469
- Buskey EJ (1998) Energetic cost of swarming behavior for the copepod *Dioithona oculata*. *Mar Biol* 130:425–431
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton
- Christensen-Dalsgaard KK, Fenchel T (2003) Increased filtration efficiency of attached compared to free-swimming flagellates. *Aquat Microb Ecol* 33:77–86
- Davis CS, Alatalo P (1992) Effects of constant and intermittent food supply on life-history parameters in a marine copepod. *Limnol Oceanogr* 37:1618–1639

- Dewsbury DA (1982) Ejaculate cost and male choice. *Am Nat* 119:601–610
- Doall MH, Colin SP, Strickler JR, Yen J (1998) Locating a mate in 3D: the case of *Temora longicornis*. *Phil Trans R Soc B* 353:681–689
- Fenchel T, Jonsson PR (1988) The functional biology of *Strombidium sulcatum*, a marine oligotrich ciliate (ciliophora, oligotrichina). *Mar Ecol Prog Ser* 48:1–15
- Frost BW, Bollens SM (1992) Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. *Can J Fish Aquat Sci* 49:1137–1141
- Gerritsen J (1980) Sex and parthenogenesis in sparse populations. *Am Nat* 115:718–742
- Hedenström A, Ålerstam T (1993) Optimal flight speed of birds. *Phil Trans R Soc B* 348:471–487
- Hedenström A, Ålerstam T (1996) Skylark optimal flight speeds for flying nowhere and somewhere. *Beh Ecol* 7:121–126
- Hirst AG, Kiørboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. *Mar Ecol Prog Ser* 230:195–209
- Hopkins CCE (1982) The breeding biology of *Euchaete norvegica* (Boeck) (Copepoda, Calanoida) in Loch Etive, Scotland – assessment of breeding intensity in terms of seasonal cycles in the sex-ratio, spermatophore attachment, and egg-sac production. *J Exp Mar Biol Ecol* 60:91–102
- Ianora A, Poulet SA (1993) Egg viability in the copepod *Temora stylifera*. *Limnol Oceanogr* 38:1615–1638
- Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Mar Biol* 139:587–596
- Johansen JE, Pinhassi J, Blackburn N et al. (2002) Variability in motility characteristics among marine bacteria. *Aquat Microb Ecol* 28:229–237
- Kerfoot WC (1978) Combat between predatory copepods and their prey – Cyclops, Epischura, and Bosmina. *Limnol Oceanogr* 23:1089–1102
- Kiørboe T (2006) Sex, sex-ratios, and the dynamics of pelagic copepod populations. *Oecologia* 148:40–50
- Kiørboe T (2007) Mate finding, mating, and population dynamics in a planktonic copepod *Oithona davisae*: there are too few males. *Limnol Oceanogr* 52:1511–1522
- Kiørboe T, Bagøien E (2005) Motility patterns and mate encounter rates in planktonic copepods. *Limnol Oceanogr* 50:1999–2007
- Kiørboe T, Møhlenberg F, Hamburger K (1985) Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and the composition of specific dynamic action. *Mar Ecol Prog Ser* 26:85–95
- Kokko H, Rankin DJ (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Phil Trans R Soc B* 361:1615–1638
- Kokko H, Wong BBM (2007) What determines sex roles in mate searching? *Evolution* 61:1162–1175
- Loose CJ, Dawidowicz P (1994) Trade-offs in diel vertical migration by zooplankton—the cost of predator avoidance. *Ecology* 75:2255–2263
- Mauchline J (1998) The biology of calanoid copepods. *Adv Mar Biol* 33:1–710
- Menden-Deuer S, Grünbaum D (2006) Individual foraging behaviors and population distributions of a planktonic predator aggregating to phytoplankton thin layers. *Limnol Oceanogr* 51:109–116
- Mengl L, Orsi JJ (1991) Selective predation by larval striped bass on native and introduced copepods. *Trans Am Fish Soc* 120:187–192
- Morris MJ, Gust G, Torres JJ (1985) Propulsion efficiency and cost of transport for copepods: a hydromechanical model of crustacean swimming. *Mar Biol* 86:283–295
- Nesbitt BF, Beevor PS, Cole RA, Lester R, Poppi RG (1973) Pheromones of 2 noctuid moths. *Nat New Biol* 244:208–209
- Nihongi A, Lovern SB, Strickler JR (2004) Mate-searching behaviors in the freshwater calanoid copepod *Leptodiaptomus ashlandi*. *J Mar Syst* 49:65–74
- Norberg Å (1981) Optimal flight speed in young birds when feeding young. *J Anim Ecol* 50:473–477
- Ohman MD, Wood SN (1996) Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. *Limnol Oceanogr* 41:126–135
- Ohtsuka S, Huys R (2001) Sexual dimorphism in calanoid copepods: morphology and function. *Hydrobiologia* 453/454:441–466
- Olsson M, Madsen T, Shine R (1997) Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proc R Soc Lond Ser B* 264:455–459
- Ruxton GD, Bailey DM (2005) Searching speeds and energetic feasibility of an obligate whale-scavenging fish. *Deep Sea Res Part I* 52:1536–1541
- Saiz E, Calbet A, Broglio E (2003) Effects of small-scale turbulence on copepods: the case of *Oithona davisae*. *Limnol Oceanogr* 48:1304–1311
- Salonen K, Sarvala J, Hakala I, Viljanen MI (1976) The relation of energy and organic carbon in aquatic invertebrates. *Limnol Oceanogr* 21:724–730
- Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect. *Oikos* 87:185–190
- Strathmann RR, Grünbaum D (2006) Good eaters, poor swimmers: compromises in larval form. *Int Comp Biol* 46:312–322
- Strickler JR (1982) Calanoid copepods, feeding currents, and the role of gravity. *Science* 218:158–160
- Strickler JR (1998) Observing free-swimming copepods mating. *Phil Trans R Soc B* 353:671–680
- Svensson M (1996) Sexual selection in moths: the role of chemical communication. *Biol Rev* 71:113–135
- Svetlichny LS, Hubareva ES (2005) The energetics of *Calanus euxinus*: locomotion, filtration of food and specific dynamic action. *J Plankton Res* 27:671–682
- Tiselius P (1992) Behavior of *Acartia tonsa* in patchy food environments. *Limnol Oceanogr* 8:1640–1651
- Tiselius P, Jonsson PR (1990) Foraging behaviour of 6 Calanoid copepods – observations and hydrodynamic analysis. *Mar Ecol Prog Ser* 66:23–33
- Tiselius P, Jonsson PR, Kaartved S, Olsen EM, Jørstad T (1997) Effects of copepod foraging behavior on predation risk: an experimental study of the predatory copepod *Pareuchaeta norvegica* feeding on *Acartia clausi* and *A. tonsa* (Copepoda). *Limnol Oceanogr* 42:164–170
- Titelman J, Fiksen O (2004) Ontogenetic vertical distribution patterns in small copepods: field observations and model predictions. *Mar Ecol Prog Ser* 284:49–63
- Titelman J, Kiørboe T (2003) Motility of copepod nauplii and implications for food encounter. *Mar Ecol Prog Ser* 247:123–135
- Tsuda A, Miller CB (1998) Mate-finding behaviour in *Calanus marshallae* Frost. *Phil Trans R Soc B* 353:713–720
- Uye S-I, Matsuda O (1988) Phosphorus content of zooplankton from the Inland Sea of Japan. *J Oceanogr Soc Jpn* 44:280–286
- Uye S-I, Sano K (1995) Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. *Mar Ecol Prog Ser* 118:121–128
- Van Duren LAS, Videler JJ (1995) Swimming behavior of developmental stages of the calanoid copepod *Temora longicornis* at different food concentrations. *Mar Ecol Prog Ser* 126:153–161
- Van Gool E, Ringelberg J (1998) Light-induced migration behaviour of *Daphnia* modified by food and predator kairomones. *Anim Behav* 56:741–747

- Van Voorhies WA (1992) Production of sperm reduces nematode life-span. *Nature* 360:456–458
- Visser AW, Kjørboe T (2006) Plankton motility patterns and encounter rates. *Oecologia* 148:538–546
- Ware DM (1975) Growth, metabolism, and optimal swimming speed of a pelagic fish. *J Fish Res Bd Can* 32:33–41
- Wedell N, Gage MJG, Parker GA (2002) Sperm competition, male prudence and sperm-limited females. *Trends Ecol Evol* 17:313–320
- Yen J, Weissburg MJ, Doall MH (1998) The fluid physics of signal perception by mate-tracking copepods. *Philos Trans R Soc Lond B* 353:387–804