Motility patterns and mate encounter rates in planktonic copepods

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Abstract

   Mate encounter rates in pelagic copepods depend on the characteristics of the mate detection mechanism as well as on the motility patterns and concentrations of males and females. We describe male and female motility patterns in two species (*Centropages typicus* and *Pseudocalanus elongatus*) in which the females excrete male-attracting pheromones and in one species (*Acartia tonsa*) in which the mates are detected by hydromechanical signals. For both pheromone-producing species, male and female motilities differ strongly; males are more directionally persistent and swim as fast as or faster than the females, and only at scales exceeding several centimeters do the male motilities resemble random walk. This prevents resampling of the same volume at the scale of encounter and maximizes the rate at which males encounter female signals. In contrast, female motility patterns are more similar to random walk, even at small scales. For the species depending on hydrodynamic cues and in which detection is practically symmetrical between the mates, male and female motilities are similar and can both be described as random walk, also at small scales. We develop simple encounter models and utilize information on motility patterns and mate signaling from our own observations and the literature to estimate search volume rates for pelagic copepods ranging between 0.6–3.0 mm in length. We show that pelagic copepods are capable of searching tens to thousands of liters of ambient water for mates daily, that search capacity increases approximately with the cube of copepod length for both chemical and hydrodynamic signalers, and that these impressive mate search volume rates are sufficient to sustain populations at typical adult densities.

Pelagic copepods live in a three-dimensional environment in which the finding of mates at a sufficiently high rate for population maintenance represents a major challenge to these nonvisual millimeter-sized animals (Buskey 1998; Lonsdale et al. 1998). However, pelagic copepods have developed mechanisms to enhance mate encounters. These mechanisms include the ability of males to remotely locate receptive females from chemical and/or hydromechanical signals (Katona 1973; Griffiths and Frost 1976; Lazzaretto et al. 1994). Remote detection of mates has been described for several species, and three different mechanisms of mate finding among pelagic copepods have been documented (Bagøien and Kiørboe in press *a*). In some species, the female leaves a pheromone trail in her wake, which can be found and followed by the male (Doall et al. 1998; Tsuda and Miller 1998; Yen et al. 1998). In other species the female moves very little and the pheromone appears to be spread into a near-spherical plume rather than a trail (Nihongi et al. 2004; Kiørboe et al. in press), and a male encountering the plume may be directed to the female. Other species again seem to rely on hydromechanical cues, and here the partners appear to detect one another almost simultaneously (Strickler 1998; Bagøien and Kiørboe in press *b*; Doall et al. pers. comm.).

A mechanistic understanding of signal generation and dispersion has been established for several species and comprises both chemical and hydromechanical communication, which has enabled development of models to describe remote location of mates (Yen et al. 1998; Bagøien and Kiørboe in press *a,b*; Kiørboe et al. in press). However, mate finding efficiencies, expressed in terms of encounter rates or as volumes of water searched for mates per unit time, are not available in the literature. Such estimates are obviously important for assessing population dynamical implications of limitations in mate search capability (Gerritsen 1980) and for evaluating whether additional mechanisms to chemical and hydrodynamic signaling are needed to secure population propagation.

Mate encounter rates depend on the efficiency of remote mate detection, on the swimming speeds and patterns of primarily the males, as well as on the concentrations of males and females. We examine motility patterns of three species of adult copepods that represent each of the three modes of mate detection previously described: *Centropages typicus,* in which the female leaves an odor trail in her wake (Bagøien and Kiørboe in press *a*); *Pseudocalanus elongates,* in which the female produces an odor cloud rather than a trail (Kiørboe et al. in press); and *Acartia tonsa,* in which the mates locate and identify each other by means of hydromechanical signals (Bagøien and Kiørboe in press *b*). We present simple mate encounter models, and based on the observed motility patterns and insights regarding the mechanisms of remote mate detection, we estimate actual search capacities for mates. We show that millimeter-sized pelagic copepods may search tens to thousands of liters of water for mates daily, that search volume rate scales with copepod size in a consistent manner regardless of the particular mechanism employed for remote mate detection, and that the estimated search volume rates lead to a sufficient number of mate encounters to allow population maintenance.

Encounter models

Male–female encounter rates (E) can be described as:

$$E = \beta C_M C_F$$

where C_M and C_F are the concentration of males and females,

respectively, and β is the search volume rate (i.e., the volume of ambient water that a male can search for females per unit time, or vice versa). For copepods employing pheromone signaling, the search volume rate depends on the shape and extension of the region within which the male can perceive and track down the female as well as on the motility pattern of primarily the male. For species using hydrodynamic signals, the search volume rate depends on the extension of the detection region as well as on the motility of both sexes. For simplicity, in species in which the female releases pheromones, we distinguish between an elongated, ellipsoid odor trail as produced by some copepods, and a more spherical odor plume, as produced by others. For species detecting mates from hydromechanical signals, we assume that both males and females can be represented by a detection sphere.

Different male motility patterns imply different mate encounter probabilities. The more directionally persistent a male swimming path, the higher the encounter rate at a given swimming velocity; and the more convoluted the male path, the lower the mate encounter rate. The motility pattern and degree of directional persistence can be characterized by examining how the net travel distance increases as a function of time. Specifically, for a population of moving copepods, the root–mean-square net distance traveled (*RMS-distance*) will be a power function of the elapsed time (T),

$$RMS\text{-}distance = aT^b \quad (1)$$

Generally, the lower the power b, the higher the extent of resampling of ambient water and, hence, the lower the mate encounter rate. The power will equal 0.5 for a classical random walk motility, and an equivalent diffusion coefficient of the copepods can then be estimated as $D = a^2/4$ (for a two-dimensional projection of the swimming track; Berg 1993). While at some (large) spatial scale, the motility of the copepods will converge toward a random walk, on some smaller scale the individuals will travel with a high degree of directional persistence in which $b = 1$. The spatial scale at which the power b changes from 1 to 0.5 is the 'equivalent run length' or the 'motility length scale.' It can be estimated as $3D/u$, where u is the swimming velocity (Berg 1993).

The 'length scale of encounter' (i.e., the radius of the spherical pheromone plume surrounding the female, the effective thickness of the pheromone trail, or the hydrodynamic detection distance) relative to the equivalent run length of the male has implications for the mate encounter rate. Mate search is much more efficient if the motility scale exceeds the encounter scale, because resampling of the same volume of water is then, in practice, reduced or avoided. If the male motility scale is much smaller than the encounter scale, then mate encounter rates can be estimated using diffusion theory. If, on the other hand, the male motility scale is much larger than the encounter scale, then linear swimming or cruising behavior of the male can be assumed when estimating the encounter rate. If the two scales are of similar magnitude, then the mate encounter rate is somewhere in between estimates obtained using the two extreme assumptions. Below we write simple encounter models for the different motility patterns and signal characteristics.

The search volume rate for a cruising male with an elongated female pheromone trail is given by the effective cross-

Table 1. Symbol definitions.

Symbol	Meaning	Dimensions
β	Encounter kernel or search volume rate	length³ time⁻¹
C_M, C_F	Concentration of males or females	length⁻³
D_P, D_M, D_F	Diffusion coefficients of pheromones, males or females	length² time⁻¹
E	Mate encounter rate	length⁻³ time⁻¹
L	Length of pheromone trail	length
r	Radius of pheromone cloud	length
S	Sensory reach of copepod	length
T	Time	time
u	Male swimming velocity	length time⁻¹
v	Female swimming velocity	length time⁻¹

sectional area of the trail (Jackson and Kiørboe 2004; Bagøien and Kiørboe in press *a*), multiplied with the male swimming velocity:

$$\beta_{\text{Trail,cruiser}} = 2Lu_{2D}\left(\sqrt{\frac{D_pL}{v}} + S\right) \quad (2)$$

where S is the sensory reach of the copepod (here approximately the length of one antennule), L is the length of the pheromone trail, D_P is the diffusion coefficient of the pheromone, v is the swimming velocity of the female, and u_{2D} is the component of male swimming velocity perpendicular to the direction of the female trail (symbol explanation in Table 1). Assuming random swimming directions of males and females, this component is, on average, equal to the average two-dimensional projection of the male swimming velocity.

The search volume rate for a 'diffusing' male searching for an elongated pheromone trail may be estimated by assuming that the trail has the shape of an ellipsoid of length L and of maximum width $2[S+(4D_PL/ev)^{0.5}]$ (Bagøien and Kiørboe in press *a*). For $L \gg$ the maximum width of the trail, the search volume rate is (Berg 1993):

$$\beta_{\text{Trail,diffuser}} = \frac{2\pi D_M L}{\ln\left(\dfrac{L}{S + \sqrt{4D_PL/ev}}\right)} \quad (3)$$

where D_M is the equivalent diffusivity of the males and $\mathbf{e}$ is the base of the natural logarithm.

Similarly, for a 'diffusing' male and a spherical pheromone plume, the search volume rate is (Berg 1993):

$$\beta_{Sphere,diffuser} = 4\pi D_M r \quad (4)$$

where r is the radius of the pheromone sphere; and for a cruising male and a spherical pheromone plume, it is:

$$\beta_{Sphere,cruiser} = \pi r^2 u \quad (5)$$

Finally, search volume rates for two diffusing (Berg 1993), respectively, cruising spheres (Evans 1989), applicable to species with hydrodynamic detection, are:

$$\beta_{2\,Spheres,diffusers} = 4\pi(D_M + D_F)S \quad (6)$$

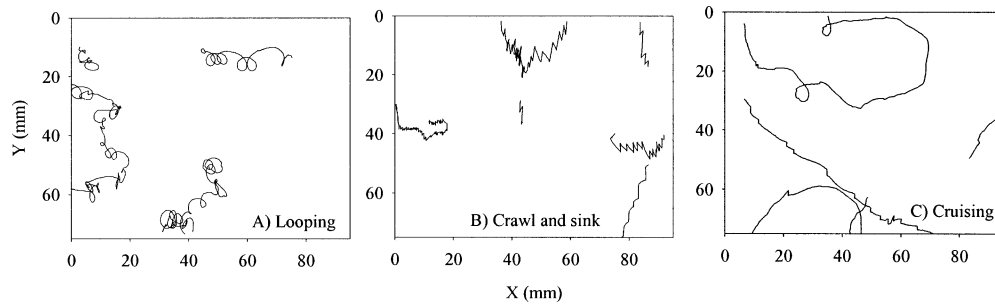$$\beta_{2\,Spheres,cruisers} = \pi S(u^2 + v^2)^{0.5} \quad (7)$$

Fig. 1. Examples of the three types of swimming tracks in *Centropages typicus.* Positions digitized at 25 Hz. X and Y are horizontal and vertical axes, respectively.

where D_M and D_F are male and female diffusivities, respectively.

Materials and methods

Centropages typicus and *Pseudocalanus elongatus* were collected in the North Sea and established in continuous cultures in the laboratory along with our already-available culture of *Acartia tonsa.* The cultures were kept at 14–18°C on a mixed phytoplankton diet of *Rhodomonas baltica* and *Thalassiosira weissflogi.* Only recently matured individuals were used for experiments. Males and females for video experiments were isolated from the culture and from each other 1–3 d prior to the experiments. During this period, and while filming, copepods were fed surplus concentrations of *R. baltica.* Replicate video recordings were conducted for each species.

Motility patterns of male and female copepods were examined separately by video recording ca. 20 copepods swimming in a 1-liter aquarium ($10 \times 10 \times 10$ cm³). The aquarium was illuminated from the back by infrared light from a LED that was collimated through a condenser (30×30 cm²). The collimated light implies that the same length calibration applies to all parts of the aquarium. The video camera overlooked the entire volume of the aquarium from the side and was connected to a monitor and a VCR. Animals were acclimatized in the aquarium for ½ h before several hours of swimming activity was recorded. Four-minute film sections in which most of the animals were swimming clear off the aquarium walls were selected for analysis. These sections were transferred to a computer, and two-dimensional projections of the swimming tracks were digitized using LabTrack software (BioRas, Kvistgård). Fifty to two hundred swimming tracks were analyzed for each sex and species.

Results

Motility patterns—For *C. typicus,* three different motility types were found for both males and females; swimming in near helical loops, cruising along more-or-less straight paths, or 'crawl and sink' motility, in which short periods of passive sinking alternate with short periods of (typically) upward-directed swimming (Fig. 1). The time spent on each motility type varied between sexes, with males primarily cruising and females spending most of their time swimming in helical loops (Table 2). Sinking velocities were consistently about 2 mm s^{-1}, while cruising and loop speeds were slightly higher in males than in females, ca. 6 and 5 mm s^{-1}, respectively (Table 2). Note that all speeds have been calculated from two-dimensional projections. While this represents the true value for sinking velocity, real cruise and loop speeds are underestimated. If we assume overall isotropic swimming directions, three-dimensional velocities are, on average, 22% higher than those recorded in two dimensions (can be shown from Pythagoras) (Table 3).

Swimming patterns in *P. elongatus* also differed significantly between the two sexes (Fig. 2). Females were swimming very slowly, almost hovering most of the time, moving along more convoluted tracks than the males, which were cruising at substantially higher velocities and along smoother tracks (Table 3). In *A. tonsa,* swimming velocities (Table 3) and swimming patterns (Fig. 3) were similar for the two

Table 2. Time budget and swimming velocities (two-dimensional projections) of *Centropages typicus.*

Motility type	Crawl-sink	Sink	Cruise	Loop	
Males					
Fraction of time spent	0.28	0.17	0.67	0.04	
Velocity±SD mm s^{-1}	—	1.9±0.3	5.6±2.2	5.5±1.8	Overall average 4.7±2.3
Females					
Fraction of time spent	0.09	0.07	0.20	0.72	
Velocity±SD mm s^{-1}	—	2.1±0.3	4.7±1.6	5.0±1.4	Overall average 5.3±2.0

Table 3. Motility characteristics and mate encounter length scales in three copepod species. Equivalent diffusion coefficients were estimated by fitting square-root relations to the data in Fig. 3 and equating the leaf coefficient with $2D^{0.5}$. The motility length scale (=equivalent run length) was computed as $3D/u$. The encounter length scale was estimated as one antennal length for the trail-tracking *Centropages hamatus,* as the radius of the pheromone plume for *Pseudocalanus elongatus* (Kiørboe et al. in press), and as the male–female ($\male-\female$) detection distance in *Acartia tonsa* (Bagøien and Kiørboe in press *b*).

Species	Sex	Average 3-d velocity (mm s^{-1})	Equivalent diffusion coefficient, D (mm^2 s^{-1})	Motility length scale (mm)	Encounter length scale (mm)
C. typicus	♂	5.7	—	>40	
	♀	6.5	8.1	3.7	~1.5
P. elongatus	♂	5.4	—	>25	
	♀	1.7	2.0	3.5	8
A. tonsa	♂	3.9±1.1	3.2	2.5	
	♀	3.8±0.6	3.2	2.5	7

sexes, with short feeding bouts interrupted by jumps and occasional longer periods of inactivity (sinking). Periods of sinking were more pronounced among females, which tended to aggregate near the bottom of the aquarium.

Cruising, diffusing, and motility length scales—Plots of root–mean-square net distance traveled as a function of time varied between species and sexes (Fig. 4). Males showed a significantly higher degree of directional persistence than females in the two species with pheromone communication; here, the net RMS-distance traveled increased almost linearly with time up to scales of >40 mm in *C. typicus* and >25 mm in *P. elongatus.* Thus, equivalent run lengths are at least of this magnitude and are therefore much longer than the encounter scales for the two species (Table 3). Therefore, in the hunt for females, males of these species may be considered cruisers. Female motilities were close to random walk; net RMS-distance traveled increased almost with the square root of time. Equivalent diffusivities, estimated by fitting square-root relations to the data in Fig. 4 and equating the lead-coefficient with $2D^{0.5}$, were 2–8 mm^2 s^{-1} (Table 3).

Equivalent female run lengths were 3–4 mm (i.e., on the same order as encounter scales).

The motility patterns of male and female *A. tonsa,* as characterized by how the net RMS distance increased with time, were similar, and both followed approximately a square-root relation (Fig. 4). Estimated motility length scales were similar to the encounter scale (Table 3). Thus, *A. tonsa* can neither be considered to be a true 'cruiser' nor a 'diffuser' in its search for mates, but rather is something in between.

Mate encounter rates—Mate search volume rates can now be estimated on the basis of the motility characteristics (Table 3) and signal features (Table 4) of the three examined species. Since male motility scales substantially exceed encounter scales in the two species using chemical communication, *C. typicus* and *P. elongatus,* the model for search volume rates assuming a cruising behavior of the searcher applies (Eqn. 2 and 5). For *A. tonsa,* depending on hydromechanical detection of mates, accurate mate search volume rates cannot be estimated, since the encounter and motility scales are similar. The correct value will here be somewhere
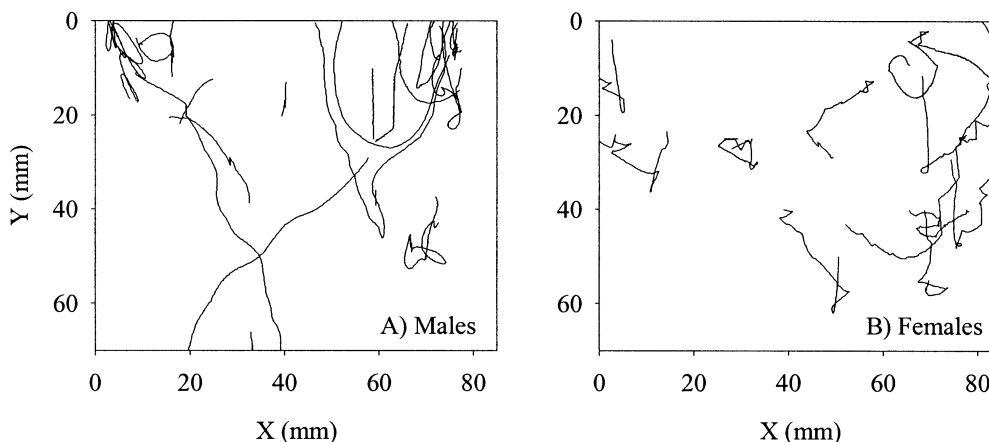

Fig. 2. Examples of swimming tracks of male and female *Pseudocalanus elongatus.* Positions digitized at 25 Hz. X and Y are horizontal and vertical axes, respectively.
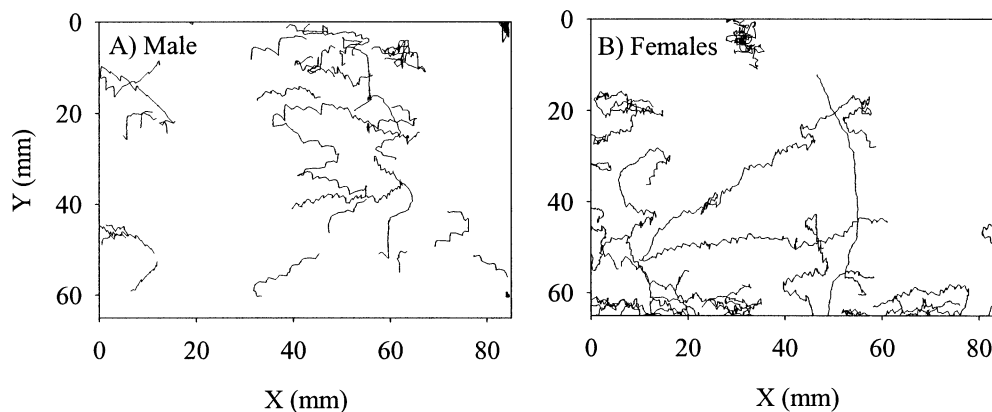
Fig. 3.   Examples of swimming tracks of male and female *Acartia tonsa*. Positions digitized at 25 Hz. X and Y are horizontal and vertical axes, respectively.

between the estimates obtained by using the two extreme models for search volume rate (Eqs. 6 and 7). For the two species using pheromone signaling, males are capable of searching 100–200 liters of ambient water daily for females. For the species relying on hydrodynamic communication, search capacity is lower, somewhere between 50–70 L d^{-1}

Discussion

Swimming behavior—Elevated rates of predation mortality may be associated with feeding (Tiselius et al. 1997) and mating activities in copepods (Maier et al. 2000). Such behaviors may therefore reflect conflicts between different objectives. Specifically, motility patterns have implications for the rates at which predators, prey, and mates are encountered and are therefore likely to be adaptations to optimize the fundamental undertakings and trade-offs of surviving, feeding, and reproducing. Here we discuss possible adaptations of the observed motility patterns, with emphasis on mate encounter rates.

In both species using chemical signaling for remote detection of mates, *C. typicus* and *P. elongatus,* male and female motility patterns were very different. Mate finding in these species is asymmetric in the sense that the mates play different roles: the female produces a pheromone signal, the male detects the signal and is able to locate the female. In *A. tonsa,* relying on hydrodynamic signaling, mate finding is more symmetric. Both the male and the female appear to

be aware of the partner's position prior to mating, as indicated by series of 'synchronous hopping' (Bagøien and Kiørboe in press *b*), although it is the male that responds first upon detecting its partner, with a delay of only 9–12 ms between the initiation of the female and male hop (Doall et al. pers. comm.). In *A. tonsa,* the two sexes display similar swimming patterns.

Thus, for mate encounters in species using chemical communication, one has to consider separately (1) the female motility pattern that leads to the most 'encounterable' and sustainable pheromone trail or plume and (2) the male motility pattern that leads to the highest trail or plume encounter rate. The consistent difference in swimming patterns between males and females in both pheromone-producing species is unlikely to be related to sexual differences in feeding behavior, since in *P. elongatus* the males do not feed at all, while males of *C. typicus* do feed (Ohtsuka and Huys 2001). There are also several other reports of differing swimming patterns in male and female copepods, typically with males swimming faster than females (Uchima and Hirano 1988; Doall et al. 1998; Tsuda and Miller 1998).

In both species utilizing pheromone signaling, the male motility length scale exceeds the encounter length scale, which optimizes the encounter rate with pheromone plumes, and with the male swimming speeds equal to or higher than those of the females, thus further enhancing the encounter rates. Thus, male motilities appear to be adapted to finding females. Although analyses similar to those presented in Fig.
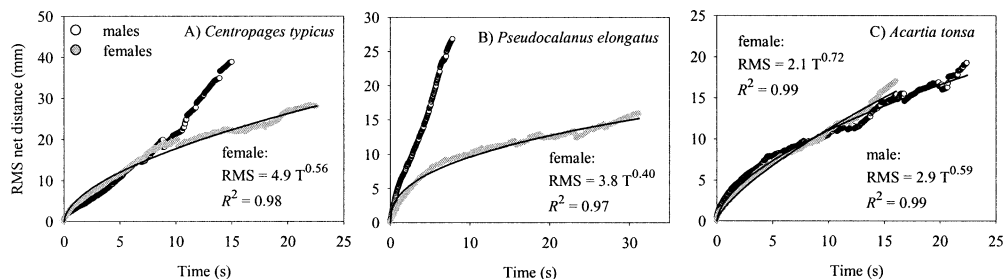

Fig. 4.   Root–mean-square (RMS) net distance traveled as a function of time in males and females of *Centropages typicus, Pseudocalanus elongatus,* and *Acartia tonsa.* Distances are based on two-dimensional projections of swimming tracks.

Table 4. Characteristics of mate finding signals. A pheromone diffusivity typical of small biological molecules, including amino acids, was assumed. All other parameters taken from Bagøien and Kiørboe (in press *a,b*) and Kiørboe et al. (in press). The Sensory reach in *Centropages typicus* was one antennula length, and in *Acartia tonsa* was the maximum male–female reaction distance. Search volume rates for *A. tonsa* were estimated, assuming both 'diffusive' and cruising behavior.

Species/signal characteristics	Cephalothorax length (mm)	Signal type	Pheromone diffusivity D_P (cm² s⁻¹)	Sensory reach S (cm)	Trail length L (cm)	Plume radius r (cm)	Search volume rate β (L-d⁻¹)
C. typicus	1.3	Pheromone trail	10^{-5}	0.15	15	—	201
Pseudocalanus elongatus	0.91	Pheromone cloud	10^{-5}	—	—	0.8	94
A. tonsa	0.8	Hydrodynamic	—	0.7	—	—	48–72

4 are not available for other species, the existing descriptions (*see* previous) indicate that this may be a more general phenomenon in species using chemical mate detection. Such fast cruising behavior, however, also implies an elevated predation risk. For the same reason that female tracks are found more efficiently by fast cruising than diffusing males, potential predators are encountered at higher rates: predation risk increases with the motility length scale and the swimming velocity. Hence, there is a trade-off between enhancing mating rate and reducing predation risk. The slower and more convoluted swimming behavior of pheromone-producing females may therefore reflect an adaptation to limit predation risk. Does this swimming pattern of the female imply a disadvantage in terms of mate encounter rates?

Theoretical considerations demonstrate that the length of a pheromone trail is independent of the swimming velocity of the female (Bagøien and Kiørboe in press *a*). Thus, it becomes the female swimming pattern rather than its velocity that determines how easily a trail is encountered and followed by a male. Intuitively, a trail with sharp bends would be difficult to follow. This is because the tracking male must continuously check the borders of the trail (Weissburg et al. 1998), and he may loose it at places of sharp turns (Doall et al. 1998; Bagøien and Kiørboe in press *a*). Thus, a pheromone trail produced by a female swimming in something like the crawl-sink pattern of *C. typicus* would be difficult to follow. Accordingly, in few of the mate encounters observed in *C. typicus* by Bagøien and Kiørboe (in press *a*) did the female swim in the crawl-sink pattern, which was also the least-displayed swimming mode in females of this species. A looped female trail is encountered with a lower probability than a straight trail by a cruising male, since some parts of the loop may 'shade' for other parts, thus decreasing the effective encounter cross section of the trail. The reduction in encounter probability depends on the pitch and radius of the helix as well as on the perceptive distance of the male (essentially the length of the antennules). From the point of view of mate encounter, female looping is thus less efficient than straight cruising. Despite this, female *C. typicus* spends much more time looping than cruising. This, however, leads to a lower diffusivity of the female, and the resulting lower risk of encountering a predator might compensate for the somewhat reduced dating success.

Pheromone clouds are only produced by hovering females that move very little. Small-scale diffusive motility of the female in combination with a feeding current and frequent changes of the body orientation efficiently help spread out the pheromone molecules around the female (Kiørboe et al. in press). Thus, the diffusive swimming behavior of *P. elongatus* females optimizes signal generation and dispersion while keeping predator encounters at a minimum.

Both sexes of *A. tonsa* had convoluted swimming tracks, with motility length scales similar to the encounter length scale, which reduces mate encounter rates. On the other hand, *A. tonsa* is particularly sensitive to hydrodynamic signals, compared to other copepods (Fields and Yen 1997; Kiørboe et al. 1999), allowing for detection of mates over relatively long distances (Bagøien and Kiørboe in press *b*). At the same time, predator avoidance is optimized, both in terms of motility behavior and in the efficiency by which approaching predators are detected from their hydromechanical signals. This would indicate that *A. tonsa* and possibly other species utilizing hydrodynamic mate signaling have solved the trade-off between reducing predation risk and optimizing mate encounter rates differently from species using chemical mate signaling.

Magnitude and scaling of mate search capability—The mate search volume rates estimated above cannot be considered to be very accurate. We have assumed, for example, that a chemical trail that is intercepted by a male is detected with a likelihood that is independent of the distance downstream the female, while in fact pheromone concentration and, thus, trail detectability declines with increasing distance (Bagøien and Kiørboe in press *a*). Moreover, in the ocean, turbulence may interfere with both chemical and hydromechanical signals (Visser 2001; Visser and Jackson 2004). In that sense, our calculations may be considered as estimates of potential search volumes. On the other hand, the strength of pheromone signals as well as swimming patterns may vary. Males have a limited spermatophore production rate and capacity (e.g., Hopkins 1982), and females have a limited need to mate. Our observations stem from animals taken from laboratory cultures in which the copepods are likely to have encountered mates already. In that respect, our search rate estimates may be conservative.

Similar reservations apply to the mate search volume rates that can be computed from information on mate encounter rates, plume and trail dimensions, detection distances, and

Table 5. Estimates of motility and mate signaling parameters taken from the literature and resulting estimates of mate search volume rates. Signal type is pheromone trail (Tr), pheromone cloud (C), or hydrodynamic (H). The search volume rate for *Diaptomus pallidus* is estimated from the average time it takes a male copepod to find a female at various female concentrations.

| Species/signal characteristics	Length (mm)	Signal type	Male 2d velocity* (cm s⁻¹)	Female 3d velocity* (cm s⁻¹)	Sensory reach S (cm)	Trail length L (cm)	Plume radius r (cm)	Search volume rate β (L d⁻¹)	Reference
Calanus marshallae	3.0	Tr	0.56	0.27	0.35	50	—	1902	Tsuda and Miller (1998)
Temora longicornis	1.0	Tr	0.80	0.59	0.12	6.5	—	117	Doall et al. (1998)
Diaptomus pallidus	1.0	Tr?	—	—	—	—	—	108	Williamson and Butler (1987)
Leptodiaptomus ashlandi	0.96	C	0.12	—	—	—	1.5	92	Nihongi et al. (2004)
Cyclops scutifer	0.60	H	0.30	0.37	0.37	—	—	19.5	Strickler (1998)

* 2d, two-dimensional; 3d, three-dimensional.
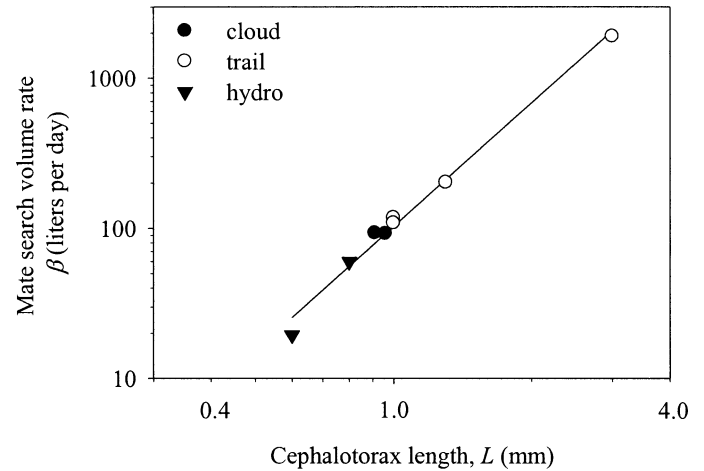
Fig. 5. Mate search volume rates, β, (L d⁻¹) as a function of female size, L, (mm), in eight species of pelagic copepods. Data from Tables 4 and 5. The regression line is log β = 2.01 + 2.73 × log L.

swimming characteristics compiled from the literature (Table 5). Despite the diversity of observational methods and circumstances, these data, together with our observations, indicate a consistent scaling of mate search capacity in copepods: search volume rates vary between tens to thousands of liter per day for millimeter-sized copepods and increase with copepod length raised to a power of about three (Fig. 5).

A scaling of this order is necessary to account for the fact that large animals are less abundant than small animals. In general terms, the biomass of organisms in the ocean is approximately constant in logarithmic length classes (Sheldon et al. 1972), which implies that size-specific abundances scale with length to a power of about −3. Thus, the increasing mate search capacity with copepod size compensates for the declining abundance of larger species in such a way that mate encounter rates should remain constant and independent of size. This makes sense, because among pelagic copepods, fecundities and spawning frequencies are largely size independent (e.g., Kiørboe and Sabatini 1994; Hirst and Kiørboe 2002), making quantitative mating requirements size independent.

Mate encounter rates and demographic implications—Mate encounter rates depend, as previously noted, on both the mate search capability as well as on the concentrations of mature adults. Some copepod species appear to aggregate at certain depth strata at the time of mating to enhance mate encounter rates, and others may even form dense swarms, which relaxes the requirement for large mate search volume rates further. However, the documented cases of mating aggregation (*see* Hayward 1981; Tsuda and Miller 1998; Park 1995, in Mauchline 1998) and in particular swarming behavior (Ambler et al. 1996; Buskey et al. 1996) are few, and even when copepods experience adult concentrations that are higher than water column averages, they are likely to depend strongly on remote mate detection and large search volume rates. The question thus becomes whether the impressive

mate search volume rates of tens to thousands of liters daily, as estimated above, are sufficient to secure population maintenance and propagation, or whether additional mechanisms—such as aggregation—need to be invoked in general.

The rate at which a female encounters males can be estimated as the product of the search volume rate and the male concentration ($\beta C_{\male}$). Typical adult male densities of 1 mm-sized copepods are on the order of >10 m^{-3} during the productive season (e.g., Marshall 1949; Digby 1951; Schnack 1978), implying male encounter rates of >1 d^{-1} for a typical value of $\beta = 0.1$ m^3 d^{-1}. Given adult longevities on the order of 10 d in 1 mm-sized copepods (Hirst and Kiørboe 2002), this implies a potential for many mating events in the lifetime of an adult female. In some species, one mating is sufficient for the entire reproductive career of a copepod, while in other species, repeated mating events are required, up to one per batch of eggs produced (e.g., Berger and Maier 2001; Ohtsuka and Huys 2001). In either case, the substantial mate search capacity demonstrated in this study for a number of copepods appears to be sufficient to prevent mating limitation from constraining population propagation during the productive season. Therefore, other mechanisms, such as spawning aggregations, need in general not be invoked.

Population maintenance during periods of low population density, typically winter, may, however, be more critical (Gerritsen 1980). Kiørboe (unpubl. data) addressed this question and demonstrated that, except in species that can survive meager seasons as resting eggs in the sediment, population maintenance of pelagic copepods depends strongly on the mate search capacity: below a certain critical population density, mate encounter rates become too infrequent to compensate for mortality losses to allow the population to survive. Therefore, the geographical distribution of a self-maintained population may eventually become constrained by the capability of the mates to find one another, and, conversely, efficient mate finding expands the geographical distribution of a species. The impressive mate search capacity of small pelagic copepods estimated in this study may, thus, help explain the relative success of copepods in the ocean, where copepods are the absolutely dominating taxonomic group in the plankton (e.g., Boxshall 1998).

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