Particle and prey detection by mechanoreceptive copepods: a mathematical analysis

Jeannette Yen[1] & Akira Okubo[2,†]
[1] *School of Biology, Georgia Institute of Technology, Atlanta, GA 30332-0230, U.S.A.*
E-mail: jeannette.yen@biology.gatech.edu
[2]*Marine Sciences Research Center, State University of New York, Stony Brook, U.S.A.*

Abstract

When particles move through fluids, they produce far-field pressure differences and near-field fluid deformations. Here we evaluate if a copepod, relying on mechanoreceptive antennulary setal hairs, can detect pressure changes caused by a variety of signal sources. We first provide a correction of the copepod mechanoreception model of Legier-Visser et al. (1986), showing how an object above a minimum size should be detectable. The pressure change ΔP created by an object of this minimum size was 385 dynes/cm^2, based on biomechanical relationships for a rigid seta bending with respect to the exoskeletal body and using the neurophysiological detection threshold of a 10 nm bend of the sensory seta (Yen et al., 1992). The ΔP for: a 3 μm particle = 0.01 dynes/cm^2, a 50 μm particle = 0.16 dynes/cm^2, an escaping nauplius = 78 dynes/cm^2, a revolving prey = 10^{-5} dynes/cm^2, a 1 mm copepod escaping at 1 m/s at a distance of 1 mm from the mechanoreceptive sensory hairs of its captor = 312 dynes/cm^2. Only the copepod escaping at high-speed close to the captor would create a pressure difference that could elicit a response. At this point, we conclude that pressure differences are rarely of a magnitude that is perceptible and that additional information must be derived for a copepod to detect prey. Other signals include fluid deformations as well as other types of stimuli (odor, shadows). Like most organisms, a copepod will rely on all sensory modalities to find food, avoid predators, and track mates, assuring their survival in the aquatic environment. It also is possible that the biomechanical model is insufficient for estimating pressure differences causing the cuticular deformation or that further analysis is necessary to improve our certainty of the sensitivity of the copepod seta.

Introduction

Particles and prey are available for consumption if the animal perceives their presence. Presence can be revealed if a signal is created. One possible signal is the pressure wave, which is produced when an object moves through a compressible fluid. This signal propagates over long distances at the speed of sound, while the major components of the other signal: fluid displacements, attenuate rapidly with distance from the source (Harris & van Bergeijk, 1962; Tautz, 1979; Kirk, 1985).

Correction of the Legier-Visser et al. 1986 model

In 1986, Legier-Visser et al. (1986) proposed a model suggesting that copepods could detect the presence of food particles by mechanoreception of pressure differences. They argued that a particle, caught within the sheared steady laminar flow in the copepod feeding current, causes a deformation in the streamlines perceivable by the copepod as patterns in pressure differences. Their model predicts that a copepod can sense intermediate sizes of sinking particles but cannot sense particles that are smaller nor particles that are larger than the preferred size. Their explanation for this relationship is that smaller particles do not make a disturbance of a magnitude that is greater than the threshold for detection while larger particles make

a pressure disturbance "of a scale much larger than the resolution scale of the mechanoreceptors of the antennae" (Legier-Visser et al., 1986). However, a larger particle always will make a more intense disturbance. By definition, once the threshold intensity or a physically-adequate stimulus is reached, the signal is perceived, and it remains perceptible with increasing signal strength unless background noise interferes or the signal is of a physiologically damaging intensity.

Reanalysis of the model shows an error in the calculation of the pressure difference, ΔP, between uninterrupted flow and flow deformed by the particle. The equation of Langlois (1964) to calculate the streamline deformation caused by a particle in the flow, as presented in Equation (1) of Legier-Visser et al. (1986), is:

$$\Delta P = \frac{(3\mu a U)\cos\theta}{2r^2}, \tag{1}$$

where μ = dynamic viscosity = 10^{-2} g cm^{-1} s^{-1}, a = particle radius, θ = angle between particle and the mechanoreceptor, and r = distance from the center of the sphere to the antenna (see Fig. 1a in Legier-Visser et al., 1986). For U, Legier-Visser et al. (1986) used the feeding current velocity. Here we use the sinking velocity of the particle within the fluid parcel entrained by the feeding current, where the sinking of the particle causes changes in the streamlines. This sinking velocity is recalculated, using the Stokes' equation for the settling velocity of a sphere:

$$U_s = \frac{2g\Delta\rho}{9\nu\rho}a^2, \tag{2}$$

where g = acceleration due to gravity, ν is the kinematic viscosity = μ/ρ, ρ = density of the water, $\Delta\rho$ = the difference in the density of the particle and that of the water.

Therefore, Equation (1) becomes:

$$\Delta P = \frac{(g\Delta\rho)}{3}\cos\theta\,\frac{a^3}{(a+\eta)^2}, \tag{3}$$

where η = distance from the forward edge of the particle wall to the antenna (as in Equation (2) of Legier-Visser et al. (1986).

Solving for η:

$$\eta = \left(\frac{a}{\Delta P}\right)^{1/2} a^{3/2} - a, \tag{4}$$

where A = constant values = $\frac{(g\Delta\rho)}{3}\cos\theta$.

Setting $\eta = 0$, we find that there is a minimum size a_{m}, for a given a, A, and ΔP, which represents the size of sinking sphere entrained in a copepod feeding
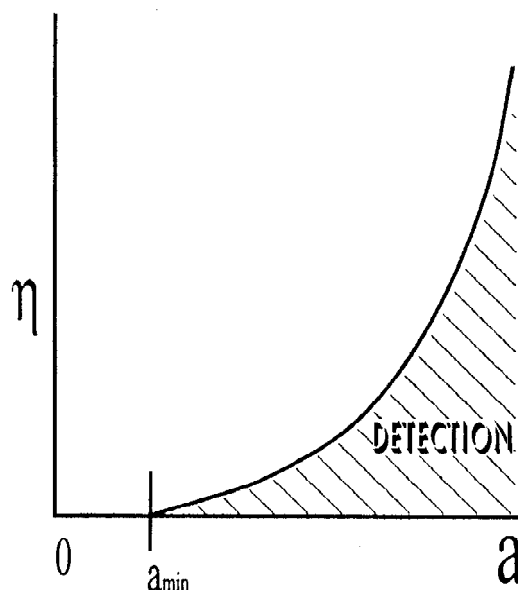

Figure 1. Graph of the solution for Equation (4), showing larger detection distances for larger particles. This is the correction to Figure 3 in Legier-Visser et al. (1986).

current that creates a pressure difference that is just above the threshold for detection at the moment the particle physically hits the copepod.

$$a_{\mathrm{m}} = \frac{\Delta P}{A} \tag{5}$$

As the particle size increases, the detection distance η increases. Hence, the new Figure 1, showing a steady increase in η vs a, replaces Legier-Visser et al.'s (1986) Figure 3.

Pressure detectors

In order to detect a pressure change such as the compressional wave, many terrestrial animals have a tympanic membrane that transduces the air-borne wave into water motion that deflect hair cells in the ear. In fish, the detection of compressional waves is facilitated by the calcareous otolith (Hawkins & Myrberg, 1983): the tissues of the fish head are essentially transparent to the passage of sound, and oscillate back and forth in phase with the long wavelengths of any low-frequency sound field. The dense otolith, of higher acoustic impedance, tends to lag behind, giving rise to shearing forces in the macula which excite the hair cells.

Does a copepod have a receptor that could sense a pressure wave? A copepod does not have an otolith.

It is possible that the oilsac, where lipid-rich energy reserves are stored, could act as a less dense fluid that moves out of phase with the copepod body. It is not known if there are stretch receptors surrounding the oilsac. Here we consider the bending of the flexible mechanoreceptive hairs of the copepod to transduce the signal into a neural impulse. Research of Yen et al. (1992) provides neurophysiological evidence that the distal setal hairs of the copepod antennule are acutely sensitive to water motion, where movement of 10 nm at a threshold velocity of 20 μm/s triggers a neural response. If the movement of water transmitting the pressure wave bends the setal hair, the wave could be detected. Since the hair is thinner and more flexible than the body of the copepod, the hair can follow the fluid flow more faithfully than the body. When such setal deflections are greater than a minimum deformation, a neural impulse is triggered and the copepod perceives the water velocity. Thus, the absolute pressure must be sufficient to give rise to motion in the seta, while not sufficient to cause the entire body to move at the same rate. A lower limit of detection occurs because very small particles do not create enough absolute pressure to move the seta. An upper limit to the size of particle occurs when the pressure change is so large that both the seta and body move, with no relative motion between the seta and body at its hinge. In cases where the pressure gradient is very steep, different setae will experience different forces and the animal will be able to derive even more information on the size and distance of the signal source.

To measure the minimum pressure difference ΔP needed to cause a nerve depolarization, physiological experiments could be performed. To give a range of ΔP to test in such physiological/behavioral assays, we provide the following values.

Detection of particles

Selecting a typically small phytoplankton particle of a size that could approximate the limit to the copepod's detection ability, $a = 3$ μm or 3×10^{-4} cm, then for $g = 980$ cm^2 s^{-1}, $\theta = 0$, and $\Delta \rho = 0.1$ g cm^{-3}, we find that:

$$\Delta P = \times ag\Delta\rho \cos \frac{\theta}{3} = 0.01 \text{ dyne/cm}^2. \qquad (6)$$

Can a copepod detect such a pressure difference? To determine this, we use measurements by Yen et al. (1992) of the neurophysiological sensitivity of antennulary mechanoreceptive setae. They found that a 10
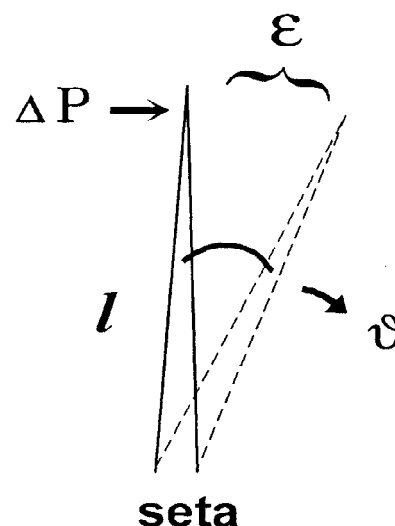

Figure 2. Biomechanical model, illustrating the bend in a seta of length l at angle φ over deformation length ϵ due to a pressure difference ΔP.

nm deflection of the seta is the minimum displacement necessary to initiate a neural response.

With this displacement threshold, we can estimate the pressure differences necessary to deflect the seta this amount. First we calculate the minimum angle of deflection (Fig. 2) needed to evoke a neural response.

$$\varphi = \frac{\epsilon}{\ell}, \qquad (7)$$

where ϵ = deformation length, ℓ = setal length. When a 1 mm seta is bent 10 nm, the threshold angle is:

$$\varphi_m = \frac{10^{-8}m}{10^{-3}m} = 10^{-5} \text{ radians.} \qquad (8)$$

Next, we consider the shear deformation in a seta due to the pressure difference (ΔP).

$$\Delta P = G\varphi, \qquad (9)$$

where G = shear modulus. G is expressed by:

$$G = \frac{E}{2(1+\upsilon)}, \qquad (10)$$

where E is Young's modulus and υ is Poisson's ratio. From Wainwright et al. (1976), a likely value for υ ~0.3. The value of E varies one-hundred fold or more. For keratin:

$$E = 3 \times 10^3 \text{Meganewton/m}^2 = 3 \times 10^{10} \text{ dyne/cm}^2$$

as given by Wainwright et al. (1976):

For resilin, found in copepod limbs (Alcarez & Strickler, 1980):

$$E = 10^7 \text{dyne/cm}^2$$

(Jensen & Weihs-Fogh, 1962, in Pedley, 1977).

For an isopod pleopod, E was empirically determined to be:

$$E = 5 \times 10^9 \text{dyne/cm}^2 \text{ (Alexander et al., 1995).}$$

The very thin cuticular seta (2–5 μm thick and wide, 10–2 mm long) of the copepod is close in composition to the isopod podite and somewhat similar in thickness (20 μm for isopod) and length (2 mm for isopod) but not in width (2 mm for isopod). It is likely the Young's modulus for the copepod seta is less than that found for the isopod pleopod but larger than that of pure resilin. To evaluate G, we use an E-value of 10^8 dyne/cm^2. Replacing the values into Equation (9):

$$G = 0.385 \times 10^8 \text{ dyne/cm}^2$$

and:

$$\Delta P_m = (0.385 \times 10^8 \text{ dyne/cm}^2)(10^{-5} \text{radians})$$
$$= 385 \text{ dyne/cm}^2.$$

As computed from Equation (6), the 3 μm particle generates a pressure difference that is below the threshold and hence cannot be detected. We can use these biomechanical relationships to calculate the length of seta needed to detect the pressure difference created by a particle entrained in the copepod feeding current. In order to detect a 50 μm particle, which produces a $\Delta P \sim 0.16$ dyne/cm^2, the seta would have to be 2 m long!

From this, we conclude that the copepod probably cannot detect particles relying on mechanoreception of the pressure difference they cause in the feeding current. The physiologically-measured physically-adequate stimulus of 10 nm of seta movement for initiating a neural response from the copepod mechanoreceptive hair is not small enough to detect pressure changes caused by particles. Species-specific differences in detection may be possible, where low sensitivity could be expected for a large predator preying on fast-moving copepods allowing them to filter out noise, while higher sensitivity would more likely be needed for smaller suspension feeders to detect finer scale and slower stimuli such as small and slow-moving particles. While species-specific differences in physiological sensitivities were not marked (Yen et al., 1992) behavioral sensitivities of the escape response to shear did show that copepods from quiet habitats (open-ocean *Euchaeta rimana*) were more sensitive than those from well-mixed regimes (surface-dwelling *Labidocera madurae*; Fields & Yen, 1997). Continued research on copepod physiological and behavioral sensitivities to water-borne signals can help to evaluate the role of prey type and habitat stability on detection capability.

It also is possible that the biomechanical model we chose to use here is inadequate for estimating pressure differences causing the cuticular deformation. This analysis assumes that the angle of deflection is important whereas other factors, such as velocity and acceleration, may be more significant cues. The elastic modulus for keratin may be too large to use for the fine setal hairs of the copepod. Furthermore, a more accurate description of this sensory system would be of a rigid seta coupled to the exoskeleton by way of a loose joint. The seta itself may bend at high forces to avoid breakage but it also can pivot as a lever arm on the joint between seta and body. It is likely that the shear modulus of the loose joint is much smaller than that of the seta, making the system much more sensitive to small forces. It is necessary to examine the performance characteristics of the setae to improve our certainty of the sensitivity of the copepod seta.

Detection of mobile prey

As concluded from the above analysis, it appears unlikely that immobile particles generate a change in the pressure field that is large enough to be perceived by the copepod. But do the movements of mobile prey like a nauplius, tintinnid, or another copepod, create a detectable change in the pressure field? For example:

(a) WAKE: What if the source of the pressure difference is a wake, cast off by an escaping zooplankter that was entrained into the copepod feeding current? The fluid disturbance in the wake has a diameter of 0.1–1 mm (Strickler, 1977; Yen & Fields, 1994; Yen & Strickler, 1996), a velocity of 1–50 cm/s, respectively (Strickler, 1975; although escape speeds of 1 m/s for a 3 mm copepod (Fields, 1996) and 1.3 m/s for a 2 mm copepod (Wilson, 2001) have been recorded), and is entrained in a feeding current of 1 cm/s. There is no density difference because it is the same water in the wake and in the feeding current. However, the velocity difference is much larger than that created by a phytoplankton sinking within the feeding current. The typical reaction distance of a predatory copepod to such hydrodynamic disturbances is 1–2 body lengths or 1–4 mm (Doall et al., 2001).

Here we use the following to estimate the pressure difference:

$$\Delta P = \frac{1}{2} U_w^2 \rho. \tag{11}$$

where U_w is the wake velocity and ρ is the water density. Since the velocity of the jet attenuates very rapidly as $\sim 1/\text{distance}^2$, we calculate U_w as:

$$U_w = \frac{U_j}{\left(\frac{r}{d}\right)^2}, \qquad (12)$$

where U_j is the original speed of the wake as it was shed from the copepod, and d is the size of the original jet.

Considering the minimum values for each parameter, such as the energy in the 50 μm wake shed by small copepod nauplius escaping at 10 mm/s, and testing if a predatory copepod can detect it 4 mm away:

$$U_w = \frac{1\text{cm/s}}{(0.4\text{cm}/0.005\text{cm})^2} = 1.6 \times 10^{-4} \text{ cm/s},$$

$$\Delta P = \frac{1}{2}(1.6 \times 10^{-4})^2(1) = 1.2 \times 10^{-8} \text{ dyne/cm}^2.$$

This is the pressure change caused by the wake moving past the predator's sensors. It is below the detection limit.

We now consider maximum values for each parameter, which would represent the energy in the wake shed by a 1 mm copepod only 1 mm away from the sensory setae of its captor, where maximum fluid velocities can be larger than the maximum escape speeds of the copepod, due to the unsteady motion generated adjacent to the locomotory appendages. Here we use a flow velocity of 1 m/s, which is equal to copepod escape speeds, recorded using high-speed videography (Wilson, 2001):

$$U_w = \frac{100 \text{ cm/s}}{(0.1 \text{ cm}/0.05 \text{ cm})^2} = 25 \text{ cm/ s.}$$

This is the speed of the jet as it passes by the predator's sensors.

$$\Delta P = \frac{1}{2}(25)^2(1) = 312 \text{ dyne/cm}^2.$$

This is the pressure change at the predator's sensor caused by the jet, which is similar to the detection threshold. The predator should respond to this signal and they do – at distances of one-to-two body lengths, similar to this detection distance plus the length of the sensory seta (~ 1 mm). The limit of detection is a 1 mm zooplankter escaping at 1 m/s only 1 mm from the sensors of the captor. This is mighty close. Recall the model we use of Alexander et al. (1995) considers the seta as a rigid cuticular rod attached to the exoskeleton. Based on this model, which may be insufficient, it is unlikely that the detection of pressure

changes contribute at all to the detection of neighboring objects. Consideration must be given to both the far-field pressure field and the near-field fluid deformation associated with moving in fluids in assessing detection threshold. Bundy et al. (1998) modeled the fluid interactions between a moving copepod and a 50 μm immobile particle, illustrating changes in the velocity field. Jiang et al. (2002) modeled the interaction between objects of similar size: 2 copepods, and evaluated the distance where the two copepods would be able to detect each other, using the threshold of Yen et al. (1992). They find that when less than 2–5 body lengths separate two copepods, the flow field distortion alters the distribution of flow pressure and shear stress, breaking the balance of forces on the mechanoreceptors – leading to bending of the sensory hairs eliciting neural responses.

Jiang et al. (2002) also provided a value for the total force exerted by the feeding current to maintain its position as 1.21×10^{-6} N over an area of 1 mm $\times$ 3 mm (Jiang et al., 1999: Fig. 3, p. 1405) or 40 dynes/cm^2. Using Equation (6), we calculate that the size of a sinking 'particle' that would exert a force equivalent to the force of the feeding current would have a radius of 1.2 cm. The effect of this sinking object would be to move the whole copepod's body. Movement of the copepod can change its capability to discern the sinking particle. Such effects could become important when the pressure change caused by the sinking particle is 10% of the body force. Based on this amount of pressure change, we calculate that a particle with radius 1.2 mm may begin to have a significant effect on the entire copepod, inducing the simultaneous movement of the copepod along with the sinking particle. The capability for the detection of particles greater than this size would decrease, thus placing an upper size limit on the use of these equations. An animal passing by such large non-moving particles may detect differences in water movement with vs. without the presence of the particle.

Even if the bend of a seta could allow the copepod to perceive a pressure wave, Zaret (1981) comments that the direction of the source of a sound wave cannot be determined because the copepod is too small and the wave travels too quickly past its sensors. The copepod would have to resolve the temporal phase difference of the wave perceived by spatially-separated receptors. However, the pressure signal travels at the speed of sound of 1500 m/sec and would cross a 1.5 mm copepod in 10^{-3} ms. If the copepod were to sense the direction of the pressure signal, it must

sense the pressure gradient with a response time of the mechanoreceptor of 10^6 Hz. While it is unlikely that a single copepod seta can react within that time frame, adjacent setae could fire one time each, separated by 10^{-6} s. This difference in timing could impart a capability to sense a traveling pressure wave. Asymmetry in the neural response to directional bends of the sensory seta also can provide information as to the direction of the signal source (Yen et al., 1992; Fields et al., 2001). Zaret suggests another way to determine the location of the signal source, where the pressure change associated with a moving zooplankter is proportional to the relative velocities of 2 animals, which is a reasonable time scale yet it still would require a detection of a pressure gradient. The bending of setal hairs also can enable the plankter to assess the direction in the vertical plane, as experiments of Meyers & Farmer (1982) show that the setal hairs of *Daphnia* serve as gravity detectors, being deflected by the water as the animal sinks. By monitoring 3-dimensional movement patterns in fluids of different density, Meyers & Farmer (1982) found the cladoceran would respond to minute density changes affecting their sinking speed, and hence concluded that the setal hairs were kinematic viscosity detectors. Strickler (1975) suggested if an alga is sensed mechanoreceptively, the animal would need to sense the boundary layer around the cells moving in the current or, if the alga moves, the copepod would need to sense the water displaced by the alga which would require a very sensitive sensory system and a means to compensate for all other water movements.

(b) PADDLE: What if the source of the pressure difference is the vibrating appendage that generates the feeding current? This second antenna has a length of 500 μm and oscillates at a velocity of 10 cm/s. If the receptor is 2 mm away, which is a typical reaction distance of a predatory copepod such as *Euchaeta* (see Yen, 1988; Doall et al., 2001), the ambient flow at this distance from the second antenna is 0.5 mm/s. Hence, $U = 0.05$ cm/s:

$$\Delta P = \frac{1}{2}(0.05)^2(1) = 1.2 \times 10^{-3} \text{ dyne/cm}^2.$$

This is below the detection threshold.

(c) VORTEX: When observing predator–prey interactions between copepods, we recorded what appears to be the remote detection of a prey by the predatory copepod *Euchaeta rimana* at a distance of 12 body lengths or about 29 mm (Fig. 3). This was noticed when the copepod abruptly changed its orientation from upward swimming to swimming in an arc at a slight angle in the direction of the prey. After
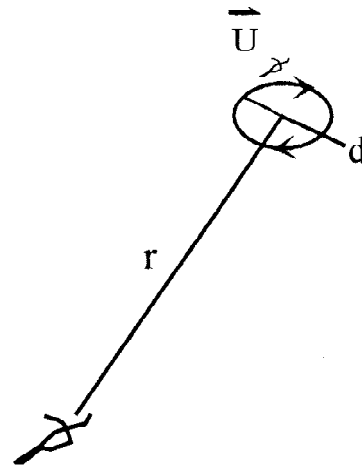

Figure 3. Detection distance r separating the predator (lower left) from a prey swimming in revolutions of diameter d at speed U, based on observations recorded in collaboration with J.R. Strickler, WATER Institute, University of Wisconsin-Milwaukee.

5–5.5 s of swimming at 6–7 mm/s, the predatory copepod captures its prey. The signal was generated by a 0.8 mm copepod (diameter of 0.3 mm), *Temora longicornis*. This smaller copepod was swimming repetitively (more than 8 revolutions at the time of detection and 4 more revolutions by the time of capture) in a vortex of the following dimensions (3.12 mm by 0.96 mm) at a swimming speed of 4.9 mm/s.

Here we, estimate vorticity ω as:

$$\omega = \frac{U}{\frac{d}{2}}, \tag{13}$$

where U = swimming speed of prey (cm/sec) and d = diameter of the vortex formed by prey (cm).

$$\omega = \frac{0.49}{\frac{0.3}{2}} = 3.3 \text{ s}.$$

The pressure at the vortex source is:

$$\Delta P_s = \frac{\omega}{v} a^3,$$

where v is the kinematic viscosity = 0.01 and a is the radius = 0.15 cm. Therefore:

$$\Delta P_s = \frac{0.33}{0.01} 0.15^3 = 1.1 \text{ dyne/cm}^2.$$

The pressure wave attenuates as $1/r^3$ (though, for a finite size source, the pressure drop may be less than $1/r^3$). For a 0.8 mm copepod:

$$\Delta P_r = \frac{1.1r}{\left(\frac{2.9}{0.8}\right)^3} = 2.5 \times 10^{-5} \text{ dyne/cm}^2.$$

This is far below the threshold.

Table 1. Calculation of the water movement D of sources of vibrations emanating from copepods (A = radius of moving appendage; U = amplitude of oscillation one body length) at the reaction distance R (1–4 mm) typifying the response of a mechanoreceptive copepod. The minimum detectable displacement D_m is 10–100 nm

Source	A (mm)	R (mm)	U (mm)	D	
Second antenna (small)	0.05	1	0.1	12.5	nm
"	0.05	4	0.1	0.2	nm
Second antenna (large)	0.1	1	0.5	500	nm [a]
"	0.1	4	0.5	7.8	nm
Copepod nauplius	0.1	1	0.2	200	nm
"	0.1	4	0.2	3.1	nm
Copepod adult	0.5	1	1.5	0.686	mm [b]
"	0.5	4	1.5	2.9×10^3	nm [b]

[a] Barely detectable.
[b] Easily detectable.
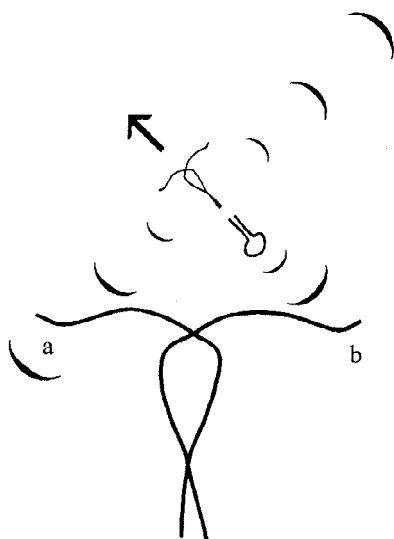$D = [A/R]^3\, U\, (\cos \theta + 1/2 \sin \theta)$; $\theta = 0°$.

Figure 4. Signals generated by a moving copepod prey as it escapes to the upper left. A vibratory signal may be perceived by sensory setae located at position (a) while jet-like wakes may be perceived by sensors at position (b) along the antennules, important sensory organs of copepods.

Signal intensity of copepod-generated vibrations

At this point, we must conclude that pressure differences are rarely of a magnitude that is perceptible and that additional information must be derived for a copepod to detect moving prey. In addition to pressure waves, another oscillating signal can be created when signals emanate from vibrating appendages or fluid sources acting as dipoles. Here we evaluate whether copepod can detect water movements created by different sources of vibrations. We calculate the signal strength of copepod movements at a distance from the source of vibrations equivalent to the reaction distance of a mechanoreceptive copepod, using Kalmijn's (1988; Fig. 4a) equation for a vibrating dipole:

$$D = \frac{A^3}{R^3} U (\cos \theta + \frac{1}{2} \sin \theta), \qquad (14)$$

where D is the water displacement generated by a dipole of radius A, vibrating at an amplitude U, at a distance R from the dipole at an angle θ from the vibrational plane (Table 1). We want to determine if that signal is above the physically-adequate stimulus. The 1–4 mm reaction distance is within the near-field range of the 1–100 Hz dipole where both fluid deformations as well as acoustic pressure waves contribute to the total velocity field (Kalmijn, 1988). The dipole movement can be created by the oscillating second antennae or the reciprocating swimming legs, which we approximate as spherical appendages or bodies with radius A. Since the antennule has an array of setal articles projecting in several directions, it is likely that a sensory seta will be oriented along the plane of the dipole ($\theta = 0°$; see Fig. 4). For $\theta = 0°$, the equation simplifies to:

$$D = \frac{A^3}{R^3} U. \qquad (15)$$

The displacements created by various sources of vibrations of a copepod are shown in Table 1.

At close range, a copepod may be able to detect the vibrations emanating from the second antennae of another large copepod. A nauplius wake barely may elicit a response but the wake of the adult copepod creates a disturbance with a signal strength higher than the physiological threshold. This agrees well with size selectivity curves showing high feeding rates on adult copepods and low feeding rates on nauplii (Yen, 1985). This signal intensity also is greater than the behavioral threshold, shown to be 2–100 times the physiological threshold (Fields & Yen, accepted). Hence, a copepod wake can evoke a behavioral response.

Most copepods react within 1–2 body lengths and the detection range need not include objects beyond this range and perhaps acoustic perception is not necessary. However, in movements of life-or-death escape decisions, the copepod 'blindly' jumps into water at distances of more than 10 body lengths. It might be advantageous that a copepod detects stimuli from this distant sector to warn them of the position of

a planktivorous fish. We find that *Euchaeta rimana* shows a remarkable degree of accuracy (Doall et al., 2001) of fast predatory lunges (142 mm/s; Yen, 1988) that suggests prior knowledge of the prey's presence and location in 3 dimensional space. Possible remote detection of the vibratory component of the prey's movement could provide the initial signal that alerts the predator to the presence of prey in close proximity. Vanderploeg et al. (1990) also suggested that hydrodynamic signals produced by moving prey in the very far field could alert a copepod of their presence.

Summary

This mathematical analysis coupled with one type of biomechanical model and our empirical measurements of copepod physiological sensitivities suggests that pressure differences caused by likely food particles are not detectable by copepod. Instead, prey movements with their fluid deformations are needed to surpass threshold sensitivities of copepod mechanoreceptive sensors. In addition to fluid motion, other types of signals also elicit specific responses. Chemical cues permit mate tracking (Doall et al., 1998) and the perception of light intensity guides vertical migratory rhythms (Forward, 1988). Like most organisms, a copepod will rely on all sensory modalities to find food, avoid predators, and track mates, assuring their survival in the aquatic environment.

Acknowledgements

References

Alcaraz, M. & J. R. Strickler, 1988. Locomotion in copepods: Pattern of movements and energetics of Cyclops. Hydrobiologia 167–168: 409–414

Alexander, D. E., J. Blodig & S-Y. Hsieh, 1995. Relationship between function and mechanical properties of the pleopods of isopod crustaceans. Invert. Biol. 114: 169–179.

Bundy, H. M., T. F. Gross, H. A. Vanderploeg & J. R. Strickler, 1998. Perception of inert particles by calanoid copepods: behavioral observations and a numerical model. J. Plankton Res. 20: 2129–2152.

Doall, M. H., J. R. Strickler, D. M. Fields & J. Yen, 2001. Mapping the attack volume of a free-swimming planktonic copepod, *Euchaeta rimana*. Marine Biology. 'Online Publication, DOI: 10.1007/s00227-001-0735-z'.

Fields, D. M., D. S. Shaeffer & M. J. Weissburg, 2001. Mechanical and neural responses from the mechanosensory hairs on the antennule of *Gaussia princeps*. Mar. Ecol. Progr. Ser.: 227: 173–186.

Fields, D. M. & J. Yen, accepted. Fluid mechanosensory stimulation of behavior from a planktonic marine copepod *Euchaeta rimana* Bradford. J. Plankton Res.

Fields, D. M. & J. Yen, 1997. The escape behavior of marine copepods in response to a quantifiable fluid mechanical disturbance. J. Plankton Res. 19: 1289–1304.

Fields, D. M., 1996. Interactions of marine copepods with a moving fluid environment. Ph.D. thesis. SUNY-Stony Brook.

Forward, R. B., Jr., 1988. Diel vertical migration: zooplankton photobiology and behavior. Oceanogr. mar. biol. Annu. Rev. 26: 361–393.

Harris, G. G. & W. A. van Bereijk, 1962. Evidence that the lateral-line organ responds to near-field displacements of sound sources in water. J. Acoust. Soc. am. 34: 1831–1841.

Hawkins, A. S. & A. A. Myrberg, 1983. Hearing and sound communication under water. In Lewis, B. (ed.), Bioacoustics, a Comparative Approach. Academic Press, New York: 347–405.

Jensen, M. & T. Weis-Fogh, 1962. Biology and physics of locust flight V: strength and elasticity of locust cuticle. Phil. Trans. r. Soc. B 245: 137–169.

Jiang, H., T. R. Osborn & C. Meneveau, 2002. Hydrodynamic interaction between two copepods: a numerical study. J. Plankton Res. 24: 235–253.

Kalmijn, A. D., 1988. Hydrodynamic and acoustic field detection. In Atema, J., R. R. Fay, A. N. Popper & W. N. Tavolga (eds), Sensory Biology of Aquatic Animals. Springer-Verlag, New York. U.S.A.: 83–130.

Kirk, K. L., 1985. Water flows produced by *Daphnia* and *Diaptomus*: implications for prey selection by mechanosensory predators. Limnol. Oceanogr. 30: 679–686.

Langlois, W. E., 1964. Slow Viscous Flow. Macmillan Co., New York: 137 pp.

Legier-Visser, M. F., J. G. Mitchell, A. Okubo & J. A. Fuhrman, 1986. Mechanoreception in calanoid copepods. Mar. Biol. 90: 529–535.

Meyers, D. G. & J. M. Farmer, 1982. Gravity receptors in a microcrustacean water flea: function of antennal-socket setae in *Daphnia magna*. The Physiologist 25: suppl.

Pedley, T. J., 1977. Scale Effects in Animal Locomotion. Academic Press, New York: 545 pp.

Strickler, J. R., 1975. Intra- and interspecific information flow among planktonic copepods: receptors. Verh. int. Ver. Limnol. 19: 2951–2958.

Strickler, J. R., 1977. Observation of swimming performances of planktonic copepods. Limnol. Oceanogr. 22: 165–169.

Tautz, J., 1979. Reception of particle oscillation in a medium – an unorthodox sensory capacity. Naturwissenschaften 66: 452–461.

Vanderploeg, H. A., G.-A. Paffenhofer & J. R. Leibig, 1990. Concentration-variable interactions between calanoid copepods and particles of difference food quality: observations and hypo-

theses. NATO ASI Series G20. In Hughes, R. H. (ed.), Behavioral Mechanisms of Food Selection. Springer-Verlag, Berlin: 595–613.

Wainwright, S. A., W. D. Biggs, J. D. Curry, and J. M. Gosline, 1976. Mechanical Design in Organisms. Princeton University Press, Princeton: 423 pp.

Wilson, S., 2001. Predator–prey interactions in the plankton: escape responses of three calanoid copepod species from a juvenile fish. M.S. thesis, SUNY-Stony Brook.

Yen, J., l985. Selective predation by the carnivorous marine copepod *Euchaeta elongata*: laboratory measurements of predation rates verified by field observations of temporal/spatial feeding patterns. Limnol. Oceanogr. 30: 577–595.

Yen, J., l988. Directionality and swimming speeds in predator–prey

and male–female interactions of *Euchaeta rimana*, a subtropical marine copepod. Bull. mar. Sci. 43(3): 175–193.

Yen, J., P. H. Lenz, D. V. Gassie & D. K. Hartline, 1992. Mechanoreception in marine copepods: electrophysiological studies on the first antennae. J. Plankton Res. 14 (4): 495–512.

Yen, J. & D. M. Fields, 1994. Behavioral responses of *Euchaeta rimana* to controlled fluid mechanical stimuli. (Abstr.) EOS, Trans. am. Geophys. Union 75: 184.

Yen J. & J. R. Strickler, 1996. Advertisement and concealment in the plankton: what makes a copepod hydrodynamically conspicuous? Invert. Biol. 3:191–205.

Zaret, R. E., 1980. The animal and its viscous environment. In Kerfoot, W. C. (ed.), Evolution and Ecology of Zooplankton Communities. Hanover: University Press of New England: 3–9.