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ORIGINAL ARTICLE

Directional Hydrodynamic Sensing by Free-Swimming Organisms

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Abstract Many aquatic organisms detect the presence of moving objects in their environment, such as predators, by sensing the hydrodynamic disturbances the movements produce. The resultant water flow is readily detectable by stationary organisms, but free-swimming organisms are carried with the surrounding water and may not detect the bulk surrounding flow, which limits the available information about the source. We have developed a theory that clarifies what information is contained in disturbances generated by an attacking predator that is available to a free-swimming organism and might be extracted from local flow deformations alone. The theory shows that, depending on how well the deformations can be measured in space and time, an organism can reduce the range of possible locations, speeds, sizes, and arrival times of the predator. We apply the theory to planktonic copepods that have mechanosensory hairs along a pair of antennules. The study reveals the presence of "blind spots," potential ambiguities in resolving from which of two sides a predator attacks, and whether it generates a bow wave or suction. Our findings lead to specific testable hypotheses concerning optimal escape strategies, which are helpful for interpreting the behavior of evasive prey and designing free-swimming robots with sensory capabilities.

Keywords Mechanosensing · Copepod · Predator-prey interactions · Inverse problem

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1 Introduction

Free-swimming organisms inhabit a sensory world radically different from that of organisms planted firmly on a solid substrate. The lack of a fixed frame of reference and the fact that they are carried along with the bulk flow of surrounding water compromise their ability to use conventional flow detectors to determine the strength and direction of sources of flow, which would otherwise alert them to the presence of mates, rivals, predators, and prey. A quantitative understanding of how such organisms extract information from this unusual environment is needed to provide insight into how hydrodynamic properties shape pelagic ecosystems, on which much of the world depends economically. Key to this is that an approaching object such as a predator generates hydrodynamic disturbances, which offer essential cues to its approach when visual and acoustic cues are limited (Triantafyllou et al. 2016). However, different approach parameters can produce similar signals and cause uncertainty in the organisms' perception. How they should respond to an ambiguous threat is unclear. Deducing upstream causes from the signals detected downstream is an example of a mathematical inverse problem. Exploring the inverse problem in developing a quantitative theory of hydrodynamic reception can help interpret how organisms can optimally respond to critical situations, such as a predatory attack. It can also provide lessons of interest in the design of biomimetic robots capable of sensing and responding autonomously to rapid hydrodynamic events.

Past theories of hydrodynamic reception have focused on localizing objects moving past flow sensors arrayed over a stationary body (Triantafyllou et al. 2016). The body may represent a benthic organism fixed to a substrate (Breithaupt and Tautz 1990) or a relatively large organism that does not move much in the water column in response to a moving object (Coombs and Conley 1997; Vogel and Bleckmann, 2000). The hydrodynamic signals that are generated by various objects moving in an aquatic environment have also received considerable attention (Bleckmann et al. 1991; Hanke et al. 2000; Visser 2001; vanDuren et al. 1998; Bleckmann 2008). Studies on their effects on receptors, and the magnitudes needed to elicit behavioral responses have established the sensitivity and dynamics of receptors in many aquatic organisms (Kiørboe 2013; Yen et al. 2015; Mellon 2014; Lenz and Hartline 2014; Triantafyllou et al. 2016); however, little is known about how a free-swimming organism extracts information on the location of moving objects generating the signals. A relatively small and freely suspended organism is carried with the bulk flow of surrounding water, which it thus cannot detect directly. Moreover, the organism may only have sensors along a line or in a plane, yet it faces the threat of predators in 3-dimensional space. Such organisms perceive an intriguingly ambiguous world, which is not well understood.

Here we develop a theory of decoding the hydrodynamic cues from an approaching bow-wave-generating object, such as an attacking predator, based on flows that are detectable by sensors on a freely suspended body. As an example, we have focused on planktonic copepods, small but numerous and ecologically important crustaceans—the "insects" of the world's oceans. A large variety of predators, from larval fish to whales, depend upon copepods for survival. In turn, these sightless organisms owe much of their success to an exquisite ability to utilize hydrodynamic disturbances to detect and escape from predatory attack. For the particular array of receptors copepods possess, our theory reveals the occurrence of potential "blind spots" in the perceptive space and identifies potential ambiguities in determining from which of two sides an attack comes, and it addresses the issue of determining whether a signal is generated by a "bow wave" of water pushed ahead of an approaching object, or by suction. Our findings lead to several testable hypotheses that are applicable more broadly in aquatic biology and robotics.

In aquatic organisms, water flows are almost universally detected by sensory hairs that project from the body into the surrounding flow. While modifications are found that involve different types of enclosures around the hairs [e.g., fish lateral line (Kasumyan 2003); sergestid shrimp antennae (Ball and Cowan 1977)], in most aquatic organisms the hairs project directly into the water, where they are deflected by water flows past the structure on which they are mounted (Casas and Dangles 2010). The hairs are coupled to stretch-sensitive ion channels in the membranes of sensory cells such that deflection or bending of the hairs open ion channels, electrically depolarizing the cell in what is termed a "transduction" process, which leads to controlling the triggering and rate of firing of nerve impulses destined for the central nervous system. In copepods, these sensory hairs are arrayed along a pair of exceptionally long antennules extending nearly perpendicularly from the anterior end of an elongate body (Yamaji 1976; Lenz and Yen 1993). The hairs project into the surrounding water, perpendicular to the antennular shaft and directly forward in most (but not all) cases. They are hinged at the base, which constrains them to be deflected inward or outward from the body by the component of water flow parallel to the length of the antennule. Impulses and behavioral responses can be elicited when the hairs are deflected by as little as 0.3 min of arc (Strickler and Bal 1973; Yen et al. 1992; Hartline et al. 1996; Weatherby and Lenz 2000; Lenz and Hartline 2014). With such sensitivity, this apparatus can detect and measure small water flows along the antennule, which then need to be decoded to enable appropriate responses (Kiørboe 2013; Lenz and Hartline 2014; Yen et al. 2015).

The "bow wave" of water pushed in front of and moving around an approaching large object such as a predator produces a non-uniform hydrodynamic perturbation in the surrounding medium. Flow intensity decreases with distance from the source. A small initially spherical parcel of water nearby is deformed by this flow (Visser 2001) (see diagram in Fig. 1a). For an organism of about the same density as water embedded in and carried with such a parcel, the deformation generates small local flows in the organism's reference frame that can signal the occurrence of an attack. For marine calanoid copepods, this deformation-produced flow has been identified as the proximate signal that elicits escape responses (Haury et al. 1980; Kiørboe 2013). The organism must be able to detect and analyze these flows in order to respond with an escape reaction that takes it away from their source (Lenz and Hartline 2014). Most discussions of plankton sensitivity to deformation focus on the "maximum deformation rate," which determines the greatest distance from a source of disturbance that might elicit a response (Kiørboe et al. 1999; Kiørboe 2013; Yen et al. 2015). This omits consideration of the fact that flows along different axes through the center of the deforming parcel are of different signs and magnitudes. Further, detection *per se* does not provide information on the nature and location of the threat. Since we know the

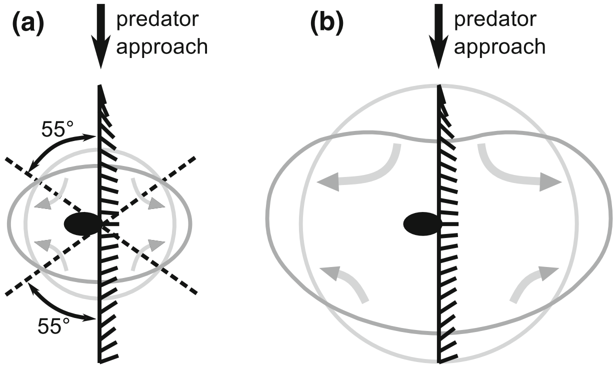

Fig. 1 Spherical parcel of water deformed by an approaching predator in the copepod's reference frame. **a** A water parcel with small radius compared with the distance to the predator compresses equally along the axis of approach and expands radially outwards in the plane perpendicular to the axis. At 55° from the axis, the parcel neither expands nor compresses. **b** A larger water parcel experiences stronger compression on the side closer to the approaching predator. Diagram represents a section through the parcel including the junction between the copepod's two antennules and the predator

type of deflection to the hairs that would lead to nerve impulses, and we know the location of the mechanosensors and the way they are deflected by flow along the antennule (Devarakonda et al. 1996), we can model that predicted flow and determine what information it contains that the copepod might be able to extract and utilize.

2 Results

Predicting the effects of an approaching large object such as a predator on the fluid flow along a copepod antennule, which will deflect and hence activate the sensory hairs, is a forward problem; the more challenging inverse problem is of predicting possible disturbances in terms of the hair deflection. To investigate the latter, the extent to which a distant object such as a predator can be localized through hydrodynamic disturbances it generates, we first develop the forward problem. To keep the analysis tractable, we model the predator by a rigid sphere of radius a moving at constant speed U. When the sphere is sufficiently large or fast, the water viscosity ν plays a negligible role in the limit of high Reynolds number $Re = 2aU/\nu \gg 1$; for example, a predator with effective diameter $2a \sim 1\,\text{cm}$ and speed $U \sim 10\,\text{cm/s}$ yields $Re \sim 1000$. In this limit, the resultant fluid flow ahead of the sphere is well described by the potential flow field $\mathbf{u} = \nabla\phi$, where the potential $\phi = -Uz - \frac{Ua^3 z}{2\sqrt{r^2+z^2}^3}$ depends on r and z, respectively, the radial and axial coordinates across and along the direction of motion (Acheson 1990). Suppose a copepod is directly in the path of the sphere: the center position of the copepod is denoted by $\mathbf{x}$ at a distance $z = Z(t)$ from the center of the sphere. For a relatively small copepod, its presence has little effect on the flow and can be neglected as is done in our model, in which case the copepod simply translates at the local flow velocity $\mathbf{u}(\mathbf{x})$ with magnitude $\dot{Z} = U(\frac{a^3}{Z^3} - 1)$, but this is undetectable by the copepod (Haury et al. 1980). Nevertheless, deformation inside the moving parcel,

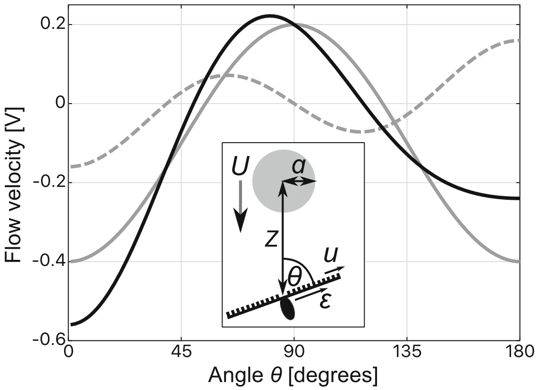

Fig. 2 Flow velocity normalized by V (black solid) at the tip of an antennule depending on its orientation angle θ. It consists of the sum of primary (gray solid) and secondary (gray dashed) flows (shown for $\varepsilon = 1/5$). Positive velocities are outward along the antennule; negative are inward. Inset shows a sphere approaching a copepod

i.e., in the frame of the moving copepod, can be detected along its pair of antennules as quantified below.

To quantify the detectable flow along each antennule, we represent the antennule by a straight line of length L extending with unit direction vector $\mathbf{n}$ from the center point $\mathbf{x}$. The flow along the antennule $\mathbf{n} \cdot \mathbf{u}(\mathbf{x} + s\mathbf{n})$ can be approximated with a Taylor expansion accurate to second order in L/Z:

$$\mathbf{u}(\mathbf{x} + s\mathbf{n}) \approx \mathbf{u}(\mathbf{x}) + s\mathbf{n} \cdot \nabla\mathbf{u}(\mathbf{x}) + \frac{1}{2}s^2\mathbf{n}^T\mathbf{H}\mathbf{n}, \tag{1}$$

where s is the distance from $\mathbf{x}$ along the antennule, and $\mathbf{H}$ is the Hessian matrix evaluated at $\mathbf{x}$. The detectable flow velocity is given by

$$V\left[\varepsilon(1 - 3\cos^2\theta) + \varepsilon^2 K(3 - 5\cos^2\theta)\cos\theta\right], \tag{2}$$

where $V = 1.5Ua^3Z^{-3}$ is a velocity scale (V/Z is a typical deformation rate), ε is the coordinate along the antennule rescaled by Z and lies in the range $0 \leq \varepsilon \leq L/Z$, θ is the angle formed between the antennule and the direction pointing from the antennule base to the approaching sphere, and $K = 2$. Equation (2) can be interpreted as the sum of two parts: $\varepsilon V(1 - 3\cos^2\theta)$, which varies linearly with ε and $\varepsilon^2 VK(3 - 5\cos^2\theta)\cos\theta$, which varies quadratically. These hereafter are referred to as primary and secondary flows, respectively. (Their dependence on θ is plotted in Fig. 2.) The primary flow is what the vicinity of the copepod experiences, with equal compression along the axis of approach and expansion in the plane perpendicular to the axis (Fig. 1a). The secondary flow is a small correction to the primary flow due to the falloff of deformation with distance from the source. The secondary flow is detectable by the distal extremities of sufficiently long antennules (Fig. 1b) but undetectable by a copepod that is too far away from the source of disturbance. Next we turn to the inverse problem of decoding the parameters a, U, Z and θ, which are all unknown *a priori*.

Decoding possible ranges of angle θ is critical for identifying suitable directions to escape away from an approaching predator, and this can be done using only the sign of

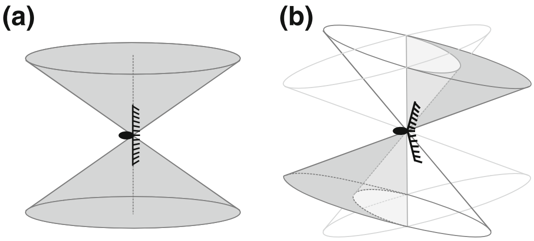

Fig. 3 Shaded regions show possible locations of an approaching predator under different conditions. **a** A copepod that detects inward flow along antennules pointing in opposite directions infers the predator to be somewhere inside the double cone; one that detects outward flow infers it to be outside the cone; it is relatively insensitive to an approach from near the margins of the cone. **b** A copepod with antennules meeting at an angle less than 180° reduces the location of the predator to a smaller subset defined in terms of two double cones. For example, if the flow is inward along one antennule and outward along the other, then the predator must be located in one double cone and not the other as shown

the primary flow in one direction. Contrary to the magnitude of the flow which depends on numerous parameters appearing in V, the sign depends only on θ: It is positive (hairs deflect outward) for $55° < \theta < 125°$ and negative (hairs deflect inward) for angles outside this range. For example, hairs along a pair of antennules oriented toward and away from the approach ($\theta = 0$; 180°) deflect inward on *both* antennules, contrary to the case with a stationary organism whose hairs all deflect in the same direction: that of the bulk flow. Whether the hairs deflect inward or outward enables a free-swimming copepod to infer two possible sectors from which the predator approaches (Fig. 3a) using a single antennule, or equivalently, a pair of antennules that are exactly 180° apart. However, the signal may be too weak to be detectable near angles for which the primary flow vanishes (55° and $180 - 55 = 125°$), which defines a "blind spot." A predator may exploit this blind spot by attacking at these angles.

The blind spot could be restricted, and a more refined estimate of the direction to the approaching object could be obtained by having two non-parallel antennules, which provide a second dimension. Then in general, at least one antennule detects nonvanishing primary flow. The sign of the flow enables inference of a smaller subset of possible locations defined in terms of two double cones with axes aligned with the two antennules (Fig. 3b). For example, if both antennules detect inward or outward flow, then the predator must be, respectively, in or out of both double cones. If the flow is inward along one antennule and outward along the other, then the predator would be in one double cone but not the other as shaded in Fig. 3b. With additional sensors distributed along a third direction off the plane of the two antennules (i.e., a "third antennule"), the possible predator locations could, in principle, be reduced further. Nevertheless, which of two opposite directions the approach comes from remains ambiguous and cannot be inferred from primary flow alone, regardless of the number of sensors, given that the primary flow exhibits cylindrical symmetry with respect to the polar axes—a predator approaching along either of the two opposite poles will produce the same deformation pattern. This produces an ambiguity similar to the one from the acoustics of fish hearing known as the "180° ambiguity" (Wubbels and Schellart 1997). However, like fish, some copepods can still successfully orient their escape to jump away from the predator (Buskey et al. 2002; Yen et al. 2015; Buskey et al. 2017). For this, additional information may be obtained from the secondary flow.

To infer from which side an approach comes (left/right, anterior/posterior, dorsal/ventral), the copepod must be close enough to the predator so as to detect the secondary flow. The secondary flow peaks in magnitude along the axis of approach: It slightly strengthens the inward hair deflection along the antennule closer to the approach and weakens it further away. The perceived signal at the tip of the antennule is generally stronger on the side closer to the approaching object. This small signal difference perceived at the ends of a pair of antennules can indicate the direction of approach and hence inform a suitable escape response, e.g., in the opposite direction. It has been observed that mechanical stimulation of single copepod antennules typically causes antennular sweeps on the stimulated side (Park 1966; Gill and Crisp 1985), which will turn the copepod away from the stimulus. Thus, the direction to the approaching body (θ) can be narrowed down without measuring the other parameters (Z, U, a). We show next how these parameters can be estimated sequentially if additional computational capabilities are available to the animal.

The distance Z to the predator can be estimated by detecting the relative strength of secondary to primary flow at an antennule tip. This can be done by comparing the flow at the tip with that extrapolated from primary flow measured in the proximal part of the antennule. The ratio of these flows deviates from unity by a small amount in the order of L/Z, which helps estimate Z in terms of antennule length L. The exact magnitude of the deviation depends on θ and vanishes when secondary flow vanishes: $\theta = 39°, 90°$, and $141°$. A predator attacking around these angles may appear farther away than it actually is. Nevertheless, the deviation is independent of V in Eq. (2), meaning that the distance to the predator can be estimated without knowledge of its speed or size.

Decoding the speed of approach of a distant predator requires detection of temporal change in water deformation. Suppose the deformation rate $E = V/Z$ along an antennule changes over time at rate $\dot{E}$. This could be computed by measuring E at two different times. While the predator–copepod distance Z is much longer than the antennule length L, the distance Z decreases approximately linearly with time like $\dot{Z} \approx -U$, a suitable approximation for most of the duration of approach (i.e., before the object is close enough to push the copepod ahead of it). Given $E \sim Z^{-4}$, we obtain $\dot{E} = 4EU/Z \approx 4E/T$, where $T \approx Z/U$ is the expected arrival time of the predator. Rearranging, the copepod can expect the arrival time to be

$$T \approx nE/\dot{E}, \tag{3}$$

where the coefficient is $n = 4$ for a predatory approach. A small T signals an imminent arrival, and this threat is detectable without knowing the predator's location or size. If the distance to the predator can be estimated as discussed above, then the speed of the predator can be estimated as well by $U \sim Z/T$.

While the size of an approaching object does not affect the decoding of θ, Z or U presented above, it may be of interest to a copepod. The object size can be estimated according to $a = (2EZ^4/3U)^{1/3}$, where E is the detected deformation rate along an antennule, Z is estimated from spatial data, and U is estimated from temporal data as described earlier.

What if the predator generates a different type of disturbance, for instance, by drawing in fluid toward its mouth? Suppose the predator remains stationary and draws in fluid toward its mouth at the origin. The resultant flow is approximated by the sink flow $\mathbf{u} = \nabla\phi$ with potential $\phi = \frac{m}{4\pi\sqrt{r^2+z^2}}$, where m is a measure of the strength of suction. For example, a suction flow with typical speed U generated in a mouth of size a would have $m = 4\pi a^2 U$. Using the same method as before, we predict that the velocity along the antennule of a copepod has the same functional form as in Eq. 2, this time with velocity scale $V = -U(a/Z)^2$ and coefficient $K = -3/2$, so the deformation rate is $E \sim Z^{-3}$. Note that V and K have switched signs; the primary flow direction simply reverses. The sink–copepod distance Z decreases with time according to $\dot{Z} = -U(a/Z)^2$ and reaches 0 in time T according to the same functional form as in Eq. (3), except that the coefficient is $n = 1$ for suction flow.

How can the copepod distinguish between a predator approaching, creating a bow wave, and a stationary one producing suction flow? One possibility, using just primary flow, is to have an organism with sensors distributed along three independent directions, which would enable inference of the approximate axis of maximal deformation and flow direction (inward or outward) along that axis. Another possibility, which requires sensing along one direction only, is to detect the curvature in temporal variations of the deformation rate. Suppose the copepod measures the second derivative of E denoted by $\ddot{E}$, which can be computed by detecting E at three different instants. Then $\dot{E}/\ddot{E}$ provides a time scale over which the deformation rate accelerates, while $E/\dot{E}$ provides a time scale over which the deformation rate increases over time. The ratio of the two time scales is a dimensionless number $E\ddot{E}/E^2$, which is either $5/4$ for a bow wave or 2 for suction flow. Thus, the copepod is capable of distinguishing between an approach and suction by computing the local slope and curvature in the deformation rate vs time curve. Finally, using secondary flow, the strongest signal will be at sensors on the antennule closer to the source of the disturbance, be it suction or an approaching object. In the case of evading a threat, this may be all the information a copepod needs to achieve an effective escape.

The analysis presented above can be readily extended to other possible disturbances, such as those generated by a food particle, which could be modeled by a sphere approaching slowly at low Reynolds number. If the copepod antennules have a negligible effect on the flow, then the flow along the antennules will have the same functional form as in Eq. (2) with a different velocity scale $V = 0.75Ua/Z$ and coefficient $K = 1$. However, in general the presence of the copepod will have a profound effect on the flow generated by a small and nearby object, a point that is often overlooked.

3 Discussion

We have considered different modes in which a copepod, with sensitive mechanosensors in a single linear array along its antennules, might be alerted to an approaching predator, such as a fish, through the bow wave produced by its approach and through suction drawing water into the fish's mouth. The antennules are not necessarily oriented along the axis of maximum deformation, and in addition, they are embedded in the bulk flow and cannot directly detect their own velocity relative to the source of disturbance, contrasting with what is commonly assumed for localizing the source through flow detection past stationary sensors (Visser 2001; Ćurčić-Blake and van Netten 2006; Goulet et al. 2008). Predator detection and localization in copepods must adequately account for the dependence on antennule orientation and sensory hair deflection as developed here.

We now discuss the relevance of our theory to the detection of predators by copepods having a threshold sensitivity in deformation rate around $E = 0.3/\text{s}$ (Burdick et al. 2007; Kiørboe et al. 1999). If a sphere of radius $a \sim 5\,\text{mm}$ approaches at speed $U \sim 100\,\text{mm/s}$ as suggested by a reviewer, the copepod is expected to be alerted at a distance in the order of $Z \sim (1.5Ua^3/E)^{1/4} \sim 20\,\text{mm}$, the exact distance depending on the antennule orientation. The distal tip of an antennule of length $\sim 1\,\text{mm}$ experiences flow with speed around $U_0 \sim 0.3\,\text{mm/s}$, again depending on orientation. This signal is stronger than any disturbance flow due to the presence of a sufficiently small copepod: If we approximate the copepod by an effective sphere of radius $R \sim 0.5\,\text{mm}$, then the disturbance flow due to inertia scales as $R^2 E U_0/\nu$ (Maxey and Riley 1983), which is in the order of 0.02 mm/s. This slip flow is reduced further around smaller copepods and nauplii, in which case they should remain embedded in the surrounding water as assumed in our theory. In other situations with substantial slip flow, our model could be extended in the future by incorporating effects on the disturbance flow due to the body's finite size, density difference, and non-uniform background flow.

From our mathematical formulation above, we can derive hypotheses as to how well a copepod might detect and how well it might then determine the direction of an approaching or attacking predator with sufficient precision to enable an oriented escape reaction that maximizes survival probability. For a distant approaching predator, the secondary flow in Eq. (2) becomes vanishingly small. Sensitivity to the primary flow generated by the bow wave is predicted to be greatest for the most distal receptors, a prediction that is confirmed by the observation that the ability to elicit escape reactions is greatly reduced in copepods with the distal tips of their antennules clipped (Gill and Crisp 1985; Yen et al. 1992). Given that the receptors are in the right sensitivity range, their ability to detect a distant approaching object is dependent on the angle, θ, that the antennules make with the axis of approach, as was developed above. This leads to the following:

Hypothesis 1 Sensitivity of the escape reaction to a distant approaching object will be minimal for an antennular angle of 55° (or 125°) to the axis of approach.

The prediction applies to distant approaching objects and not to closer ones for which secondary flow becomes significant (see below). It might thus be tested by scoring escape probability to approaching objects (predators or predator mimics) as a function of the antennular angle θ at the greater distances from which escapes can be elicited.

If the receptors are equally sensitive to flow along the antennules in either direction (distal or proximal), the copepod can only detect that a deformation has occurred. It can extract no information on the direction to the approaching object from the primary

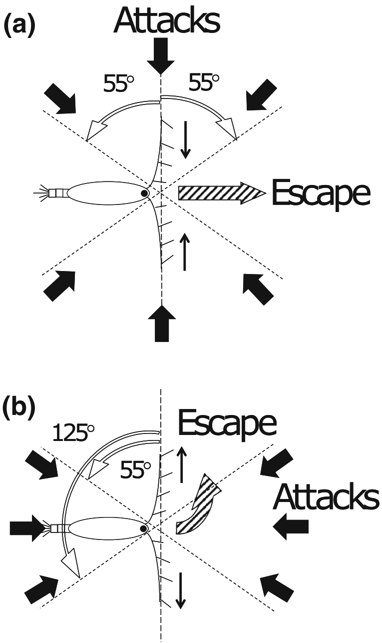

Fig. 4 Diagram of sensory hair movements and hypothesized optimal escape behavior for predatory approaches from different angles (θ in Eq. 2) to the antennule orientation (thick solid arrows). Narrow solid arrows indicate the direction of relative water flow along the antennules. **a** For an attack from an angle $0° < \theta < 55°$ with respect to the antennule axis (indicated by the two angular arc arrows subtending 55°), hairs are deflected inward (proximally); a forward escape (hatched arrow) will take the copepod out of the line of approach. **b** The situation with the attack from an angle of $55° < \theta < 125°$ to the antennules (arc arrows); in this situation, a sideways turn followed by a forward escape will take the copepod out of the line of approach (hatched arrow)

flow. If, however, the copepod can distinguish flows in opposite directions along each antennule, it can potentially determine in which of two broad sectors the axis of approach resides. Since the deformation results in a compression along that axis, then for the antennules oriented to it at angles of $0° < \theta < 55°$ (or $125° < \theta < 180°$), the sensory hairs will be deflected inward, toward the body (Fig. 4a). This condition occurs in two symmetric conical sectors centered on the approach axis, one on each side of the copepod, with the copepod heading out of the line of attack. This suggests:

Hypothesis 2 An inward deflection of sensory hairs due to an approaching distant object will produce an escape in a forward direction.

For the antennules oriented within $55° < \theta < 125°$ of the axis of approach of an object (Fig. 4b), the deformation results in an expansion along the antennule, and the sensory hairs will be deflected outward, away from the body. This is a sector forming a band encircling the copepod and centered around the antennular line. If the copepod escapes forward, it may be safe if the attack happens to be from its rear, above or below, but if from its front, it could end up in the predator's mouth. Thus, we might expect:

Hypothesis 3 An outward setal deflection due to an approaching object will produce a turn to the side, followed by an escape, out of the line of approach.

While the turning maneuver would cost extra time, it would leave the copepod directed off the line of approach. It should be noted that these predictions only require a single (properly oriented) sensor, so they could be applied to organisms with only one such. The last two hypotheses might be tested by examining the escape direction to a *retreating* object, which should be opposite from that for an advancing object since the axis of compression then becomes one of expansion.

While escape out to the line of attack is one viable strategy, some calanoid copepods are capable of escaping in a direction opposite to that of an approaching predator or predator mimic (Buskey et al. 2017), potentially an even better strategy. This cannot be explained under the assumption of sensing a simple symmetrical deformation centered on the copepod, i.e., the primary flow. Instead, the possibilities need to be considered for a role of bilateral asymmetry in the signal generated by secondary flow by an approaching object close to the copepod. This asymmetry is expected to be greatest when the antennules are aligned with the axis of approach ($\theta = 0°$, 180°) and least at three intermediate angles (Fig. 2), which suggests:

Hypothesis 4 The ability of a copepod to escape away from a nearby approaching object will be greatest when its antennules are aligned along the axis of approach and minimal when they are oriented at 39° (or 141°) and 90° to that approach.

As quantified in the angular dependence of secondary flow shown in Fig. 2, a sensor located on an antennular tip closer to a source of disturbance than one on the opposite tip will generally experience a greater deformation and hence greater water movement than one farther away. While the differential on the two sides will in general be much smaller than the deformation signal itself, if it can be detected, it could trigger the reorientation of the subsequent escape jump away from the source. This analysis suggests that the directional characteristics of an escape will shift, becoming, at most antennular angles, more precise for copepods situated closer to an approaching object.

In conclusion, we would note that this analysis has defined several features of the hydrodynamic cues generated by a predatory threat that might be extracted and utilized by an organism to inform a successful escape. We have proposed experimentally testable hypotheses for these, specifically developed for copepods but potentially applicable to other species as well. The hypotheses may not be satisfied by all species. In general, copepods such as cyclopoids, or other organisms with shorter antennules in relation to the sizes and distances of their predators, would be expected to be less sensitive to the cues, as has been noted by others (Kiørboe and Visser 1999). Among calanoids, those possessing myelinated nervous systems are better able to direct their escape reactions away from a predator mimic (Buskey et al. 2017). Myelin speeds the conduction of nerve impulses and thus permits more time for and better precision in central processing of a signal. The analysis may be applicable to other species that use hydrodynamic receptors to measure flow at different points on their body (fish lateral line (Bleckmann 2008; Stewart et al. 2014; Ćurčić-Blake and van Netten 2006; Goulet et al. 2008), shrimp antennae (Ball and Cowan 1977), squid (York and Bartol 2014), leech (Young et al. 1981), aquatic insects (Wiese 1974)). Our proposals could thus be usefully tested on a range of free-swimming species.

The current study has explored the mechanosensory world perceived by free-swimming organisms. It is potentially relevant to that of mobile free-swimming robots. Robots equipped with hair-like artificial sensors (Tao and Yu 2012) may detect local cues, which could help them navigate autonomously through an uncertain world. They may perceive ambiguities, which are inherent to sensing problems, but robots designed with sensors arrayed in only 1 or 2 dimensions may still be able to function adequately in three dimensions as presented here. The theory developed here demonstrates that simple sensory capabilities may still be sufficient to extract enough information to produce adequate responses, much like organisms surviving in nature.

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