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Chapter 8

THE SENSORY HORIZON OF MARINE COPEPODS

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ABSTRACT

The behaviors of copepods are not random. They attack prey, find and recognize conspecifics with whom to mate and they escape from potential predators. An inappropriate response can lead to a missed opportunity to feed or mate or ultimately result in death from a predator. To behave in an ecologically appropriate manner copepods must detect environmental and biological cues. Organisms derive environmental information from activity of their sensory neurons, with each individual receptor acting as a broadband filter for biologically relevant signal properties. The suite of signals an animal can detect is determined by characteristics of individual sensors and their distribution throughout the body. Because sensory neurons frequently are tuned to preferentially detect biologically significant signals, the characteristics of sensory neurons offer valuable insight into the information that governs the organism's behavior, and determine the underlying mechanisms controlling the extent and dynamics of populations. Copepods rely primarily on chemoreception [1, 2] and mechanoreception to locate prey and detect potential predators. Distance mate detection for some copepods species involves chemical trail following until the final leap when mechanoreception plays an important role. With the variety of setal morphologies on the antennae of copepods we can identify particular morphological features that narrow the range in fluid motion to which specific seta respond. While setal length and orientation affect how the setae encode basic properties such as velocity, frequency and direction, the arrangement of setae along the antennules mediate perception of more complicated properties, such as shear. These structure–function relationships provide potential insight into trophic status, predator detection abilities or distributions, and perhaps can explain the fantastic degree of variation in setal and antennule morphology. This information is also helpful for interpreting how other mechanoreceptive organisms function. For example, how the harbor seals can locate distant objects by hydrodynamic trail following [3] or how catfish track the wakes of prey [4]. However, structure–function predictions remain largely

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unverified, because we generally lack complimentary data on both the structure and ecological roles of the mechanosensory system for most aquatic organism. The purpose of this contribution is to apply current knowledge about the mechanosensory structures of marine copepods as a case study for understanding sensory ecology from a structure-function vantage point. We ask how sensor design (i.e., morphology) shapes sensor response properties and thus the behavioral and/or ecological function of particular sensor types. The focus is on planktonic copepods as model organisms for studying the role of mechanoreception because (i) they are a critical component of aquatic environments, (ii) fluid signals often act as the final proximate cue for copepod behavioral responses, and (iii) the basic properties of the copepod mechanosensory system are relatively easy to identify, and may be broadly general across a diverse range of species.

INTRODUCTION

The implicit assumptions of studying animal behavior are that organisms can discern different signals and that the uniqueness of the signals is the basis for their response. Interpreting behavior of copepods requires an understanding of the characteristics of all the potential signals, the physical and physiological response of the sensor to the fluid signal, and the relationship between the physiology and animal behavior. All information about an organism's perceivable world comes from the real-time activity of its sensory neurons. Sensory input provides organisms with a running commentary on the environmental conditions as they occur. Analyzing the string of data produced by an organism's sensors is a critical step towards understanding how organisms collect and process sensory information in order to respond in ecologically appropriate ways. Of the six common sensory modalities, touch, smell, vision, taste, hearing and magnetic orientation, only the first four appear to be important to the behavior of copepods. Numerous studies have shown that copepods respond remotely to potential mates [2,5-7], predators [8], and prey [9-12]. Although the stimuli used to identify and locate other individuals may involve a cocktail of chemical, mechanical and visual signals, previous studies show that in most cases mechanical signals are sufficient for eliciting feeding responses [11] and escape reactions [11,13-15], and are likely to be important for the final steps of mate capture [5]. These observations suggest that fluid mechanical signals convey information on the identity, the 3D location [16] as well as the relative motion of the signal source [12]. Further, recent literature suggests that for most planktonic copepods light [17] and chemical signals modulate the mechano-sensitivity of copepods but do not evoke a prey capture response or an escape reaction.

Initiating a behavioral response to a fluid mechanical signal requires a cascade of events (Figure 1). By definition for mechanoreception to occur there must be fluid motion. As an organism (prey, predator or mate) moves through the water (or water moves past the organism) it creates a fluid disturbance that imparts structure on the surrounding fluid. If the intensity of the fluid motion surpasses a mechanical threshold it causes the individual mechanoreceptor to move relative to the body. Not all motion in the mechanoreceptor will cause a neural response. Sensory perception occurs only if the displacement and the motion of the setae surpass the physiological threshold. This causes the associated neuron(s) to depolarize sending an action potential along the sensory axon. If the firing patterns surpass the behavioral threshold it causes a behavioral response. Different behaviors are initiated in

response to different patterns of sensory input. In this chapter we discuss recent advances in our understanding of the mechanosensory ability of copepods, how signals interact with individual sensors, the transduction of signals into neurophysiological signals and ultimately how this cascade of events lead to the behavior of copepods in ecologically appropriate ways.

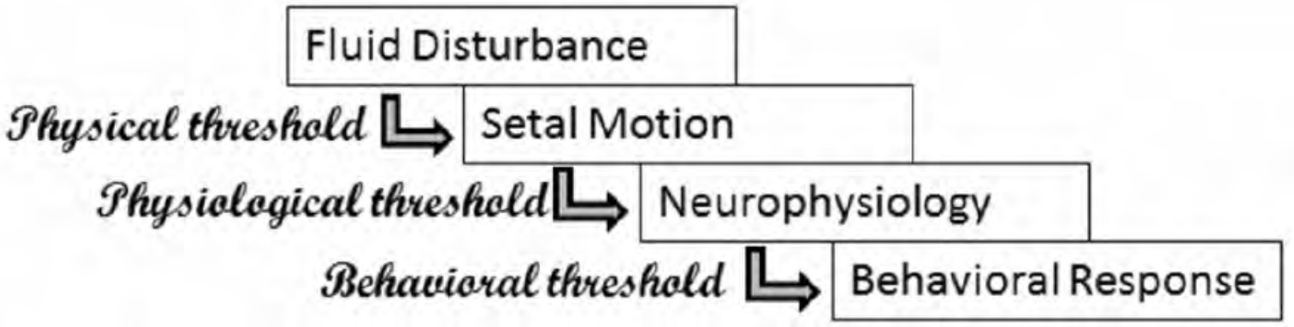

Figure 1. Sequence of events causing a behavioral response in a copepod.

STIMULUS PROPERTIES

All organisms live in a fluid environment. As they move relative to the fluid (or the fluid moves by them), they create a disturbance in the flow. Depending on the magnitude of the disturbance, the density and viscosity of the fluid and the sensitivity of the mechanoreceptor the disturbance can persist for 10s to 100s of seconds and travel centimeters to meters. Two important characteristics of fluid signals created at low to intermediate Reynolds numbers (i.e., Re < 3000) are (i) they have structure and (ii) once produced they behave in a predictable fashion that is dictated by the physical properties of the fluid (i.e., viscosity, temperature, and density). Within the past decade new visualization techniques such as PIV (particle imaging velocimetry) and highspeed video have become sophisticated and economical enough to map the complex flow fields produced by mm-sized moving animals (Figure 2). What was immediately evident is that the fluid disturbances are often orders of magnitude larger than the organisms themselves [18]. In addition the fluid motion was asymmetrical in magnitude and direction, which provided information about the location, size and speed of the source [19]. In general, fluid mechanical signals can be described by their frequency, amplitude and the initial size of the disturbance, with different organisms producing signals with different characteristics. For example, locomoting fish and large benthic crustaceans produce fluid disturbances with power spectra characterized by strong frequencies below 10 Hz with some higher frequency components (25 - 200 Hz) present in vortices shed from the caudal fins [20]. There is a growing body of literature focused on describing the fluid signals created by copepods [11,12,18,21-24]. Fluid disturbances created by swimming copepods are typically within the range of 10-50 Hz with frequencies of 30-300 Hz within the 1-2 cm in diameter small vortices release during rapid escape reactions [19]. Pulses from the independent movement of the pereiopods can achieve frequencies in excess of 500 Hz in the near-field [25]. The maximum amplitude of the disturbance is dependent on the size and behavior of the organisms. For swimming fish in the size range of 1-6 cm (the size of a typical copepod predator), the volume of water displaced due to the caudal fin motion is on the order of 0.02 ml to 3.3 ml and travels at speeds of 5 to 50 mm s^{-1}. These disturbances can be detected by copepods at a distance of over 11.8 mm. The much smaller

ciliate (*ca.* 40 um), a typical copepod prey, produce maximum fluid speeds in the range of 2-8 mm s-1 when propelling themselves through the water [12] and are detected at distances of *ca.* 0.8 mm by predatory copepods. This distance is similar to the detection of individual passive particles (50 μm polystyrene beads are detected at a distance of *ca.* 1 mm) such as phytoplankton [26]. As the fluid disturbance travels from the source, its amplitude varies inversely with the distance cubed [11,27] creating a temporal pattern to the amplitude and structure with typical deformation rates of 5 to 10 s^{-1} [18,24]. This structure is persistent for several body lengths and provides a fading footprint of the organisms that created it [28]. Mimicking these signals is critical for laboratory experiments aimed at understanding how complex fluid signals are perceived and interpreted.

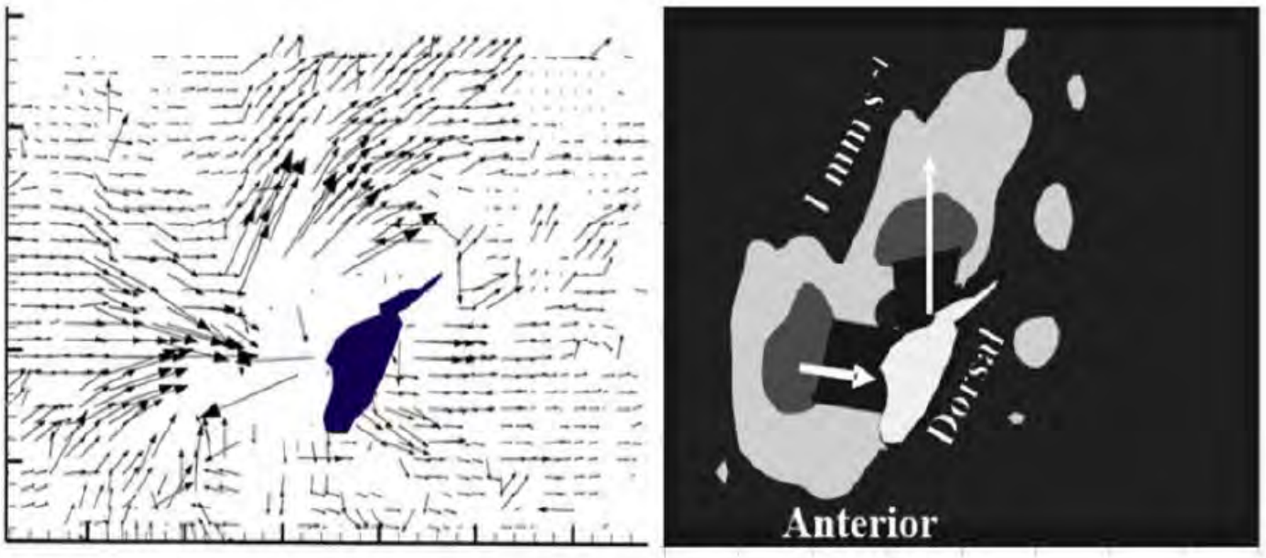

Figure 2. Left panel: particle imaging velocimetry (PIV) of the fluid disturbance created by the feeding current of an adult female *Acartia tonsa* (0.98 mm). Note how water is drawn from the region anterior and ventral to the animal and expelled ventral and posterior to the animal. *Right panel*: contours of the fluid speed of *A. tonsa*. Outer contour line marks 1 mm s^{-1}, inner contour is at 5 mm s^{-1}.

INDIVIDUAL SENSOR PROPERTIES

The literature provides several sources describing the ultra-structure of individual sensors on the antennules of copepods. Readers are directed to early work [29] for morphological characteristics of the mechanosensors, and [30] for morphological characteristics of chemoreceptors. More recent work [31] provide an excellent study on the external (SEM, light microscopy) and internal (TEM, serial section) of the setae of a deep-ocean calanoid copepod. Briefly, most mechanoreceptive setae are conical or spine shaped, with a large diameter at the base and narrowing at the tip (Figure 3). The chitinous sheath covering the antennae is continuous along the seta. The bases of individual mechanoreceptive setae are housed in an asymmetrical cuticular socket that may limit angular displacement of the sensor in a particular direction and provide protection for the setae during rapid behavioral responses when the setae are retracted along the antennule. Setal lengths within an individual animal can vary by over two orders of magnitude from short (*ca.* 10 μm) to very long (greater than 1mm) [32-35].

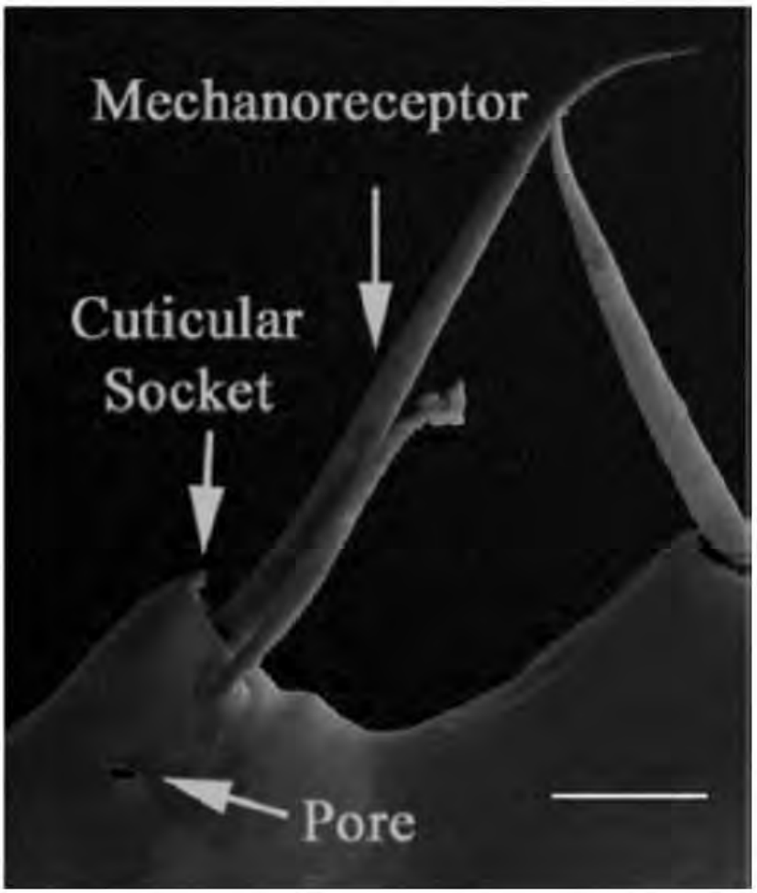

Figure 3. Setae located on the 3rd and 4th segments of *Gaussia princeps*. Note the cuticular socket housing the mechanoreceptive seta. Scale bar represents 100 μm.

The ultrastructure of the individual mechanosensory setae of the copepod is similar to the cuticular mechanosensilla of other crustaceans and arthropods. In arthropods, including the copepods, the dendrites from the associated mechanosensory neurons attach to the cuticle of the sensory hair that they innervate; for review see [36,37]. This attachment site is presumably the location where mechanotransduction occurs [33,38-40]. Fundamentally, the transduction of a mechanical signal into electrical/chemical (neurophysiological) signals requires the mechanical opening of membrane bound ion channels. The short latency of the response argues against activation of a second-messenger cascade and favors direct activation of a mechanically sensitive channel [41]. Although the exact mechanism is still unknown [31], it is hypothesized that the membrane bound channels are attached to rigid structures inside (microtubules) and outside (inner sheath cells) of the sensory cell *via* linking proteins (Figure 4). As the mechanoreceptive seta bend relative to the internal microtubules, the individual channels are pulled open *via* the linking proteins to allow the influx of positively charged ions into the membrane. This influx generates the local depolarization, which leads to the propagation of an action potential (*via* voltage gated Na ion channels; [42] in the associated axon.

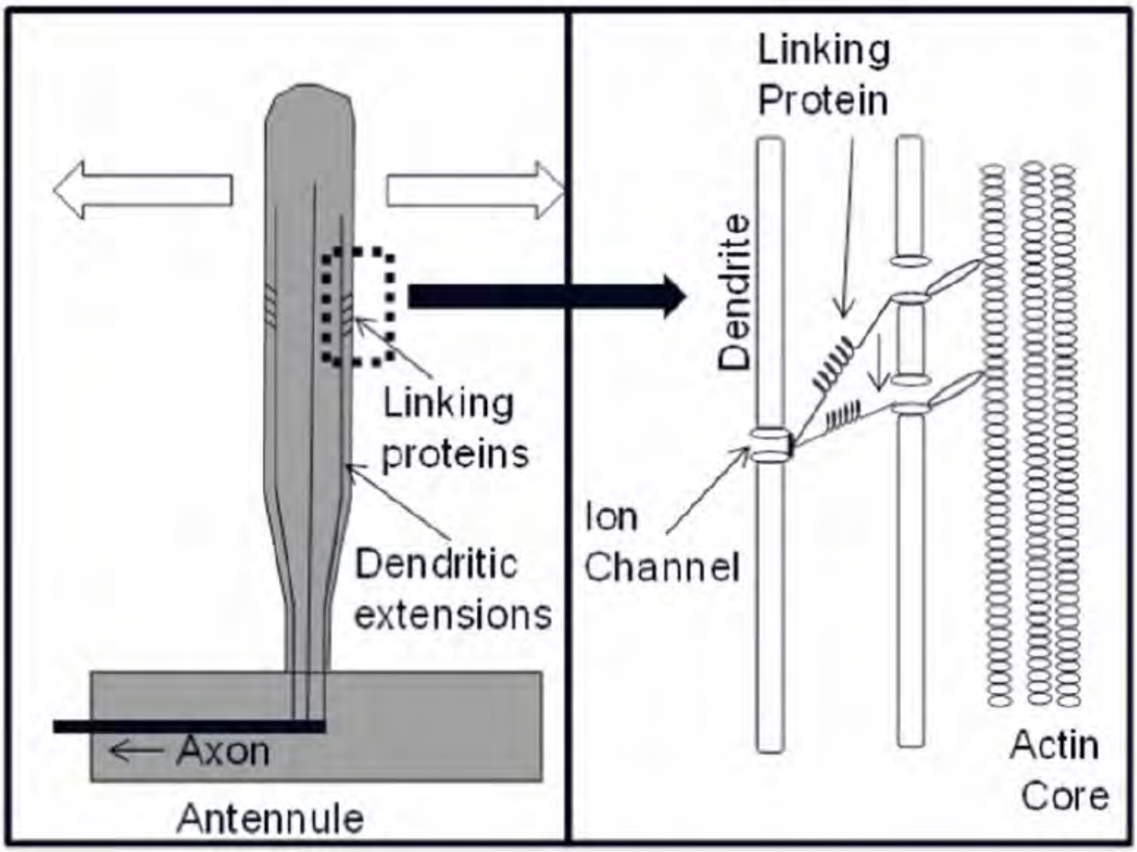

Figure 4. *Left panel*: copepod mechanoreceptive setae. When the seta is deflected to the left (white arrows), linking proteins pull open membrane bound ion channels causing local depolarization. *Right panel*: if the displacement is slow, the origin of the linking protein can move within the membrane decreasing the tension on the ion channel. If the angular displacement is rapid, the origin of the linking protein cannot move quickly enough and the channels are pulled open. Modified from [84].

There is ample evidence that the sensitivity and particular characteristics of the fluid signals detected are, in part, governed by the auxiliary structures associated with the individual neurons [35,43-45]. Across different phylum, these associated structures vary enormously in their complexity ranging from simple naked neurons to extremely elaborate structures such as those found in the mammalian ear. Slight modifications in the morphology of associated structures [46-48] or in the subtleties of their attachments [31,49] [4] [5] can give rise to a large spectrum of different stimuli that can be perceived. It is likely that the structure and function of copepod mechanosensors have been selected to maximize their effectiveness given the significant ecological consequences of perceiving (or misperceiving) mechanosensory information. As a group, copepods present a spectacular diversity of setal morphologies, orientations and degree of ornamentation [50]. The causes and consequences of this diversity remain unexplored, but the staggering degree of morphological variation suggests structure–function relationships between mechanosensor properties and their sensory roles.

PHYSICAL RESPONSES OF SETA TO FLUID MOTION

Different copepod species, genders and age classes show variations in the shape of their individual setae and in the overall configuration of their sensory array that reflect the

dominant ecological pressure (e.g., prey capture *vs.* escape) they face in their environment. Different setae respond to a given fluid stimulus with a characteristic angular displacement [35]. To fully appreciate what the sensor morphology reveals about the environment and ecological pressures faced by these animals it is imperative to characterize, in a mechanistic way, how sensors respond to quantified, biologically relevant fluid disturbances

By definition mechanoreceptors require displacement sufficient to open the associated mechanically gated ion channels to initiate a neurophysiological response [51]. Once the seta surpasses the minimum displacement threshold, the firing rate of the associated neuron provides information about the magnitude of the motion.

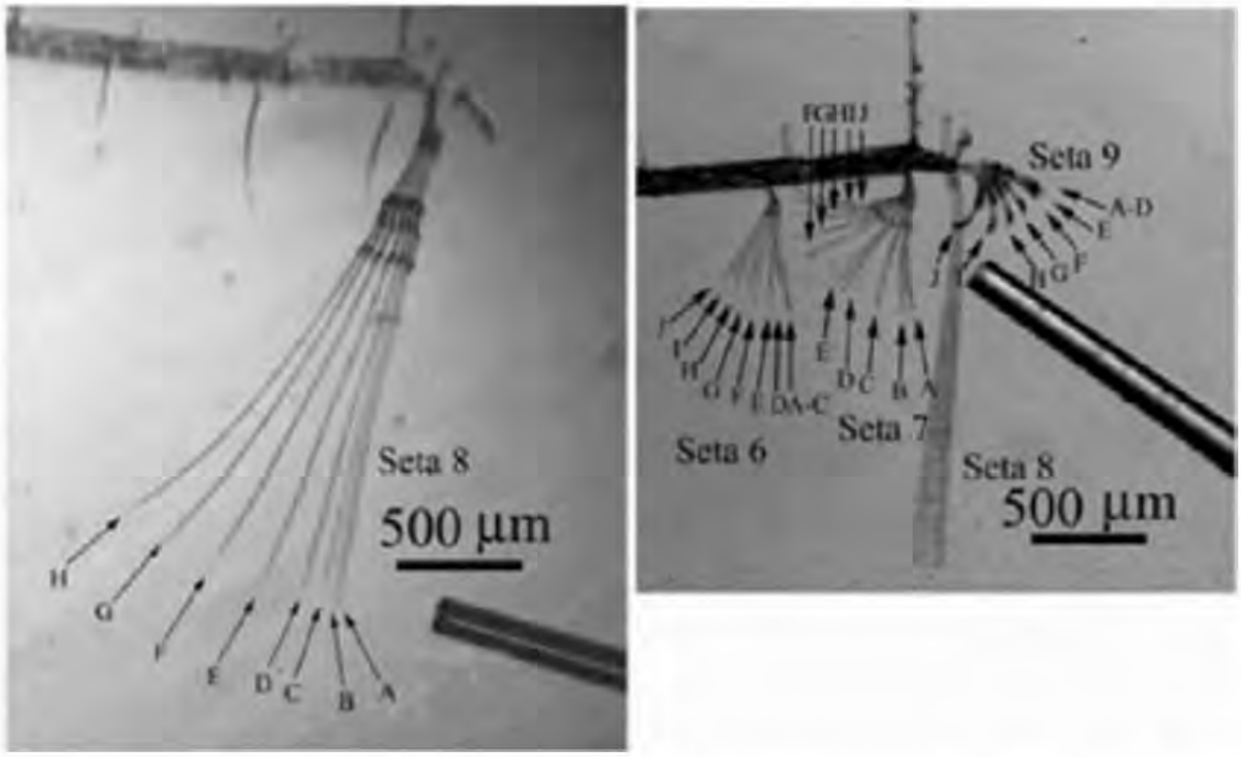

Figure 5. *Left panel*: Stimulation of the large distal setae of *Gaussia princeps* using a small water jet. Letters mark the maximum displacement of the seta at different fluid speeds. The letter "A " in both panels represents the seta orientation with no stimulation. *Right panel*: water jet is aimed at the smaller setae #7 (note that the other setae showed a delayed response).

Although only a few measurements exist, the data suggests that copepods require a minimum of 0.1 to 2.3° of angular displacement [35,42,52] to initiate an action potential in the associated nerve cell. Achieving threshold displacement depends on the velocity of the fluid (amplitude) and the duration of the pulse (frequency). However, not all setal morphologies respond similarly to the same fluid signal (Figure 5). The response a function of physical features such as the diameter and length of the seta, its mechanical properties (e.g., torsional spring and damping constant; [53]), and the viscous drag associated with the medium in which it moves [54]. For example, analytical solutions [50] (supported by experimental data [35]) show that the stimulus frequency that gives rise to the maximum angular displacement varies with the inverse of length cubed. Long setae reach the greatest maximum displacement at low frequencies while short setae respond best to high frequency stimuli. Further, since the optimal frequency is proportional to L^{-3}, small decreases in setal length give rise to large changes in the optimal frequency. One of the ramifications of this

size dependent displacement is that for a neural response to occur, the tip of the longer setae must travel further and at slower speeds. This combination leads to a longer response time for longer seta. Since rapid responses are critical to the survival of copepods [6] the use of long setae may be constrained to gathering information for behavioral responses that are relatively less time sensitive.

The physical constraints on setal bending permit a number of predictions regarding associations between setal morphology and the role of mechanosensory information. Predatory copepods that use high frequency signals from escaping prey (> 200 Hz; [11,50]) will have short setae. In contrast, copepods that detect slow moving, low frequency disturbances will have longer setae. While the optimal length might reflect the dominant signal the animal needs to detect, in reality, the complex tasks performed by most copepods involve a range of signals, and so require that they possess a complement of setal types. For instance, predatory copepods depend on the ability to detect their prey at a distance typically greater than their capture area; the larger the perceptive field, the greater the opportunity for successful capture.

Extensive perceptive fields require relatively longer, more sensitive setae, since fluid disturbances from distant sources become attenuated as they travel towards the receiver. The predator also is required to respond with directional accuracy within milliseconds when fast moving preys are within the capture region. The signals produced in close proximity to the copepod are strong, with substantial high-frequency components. Thus, predatory strikes likely depend on short setae. The relative frequency of these setal morphs may reflect the relative importance of particular signal features.

PHYSIOLOGICAL RESPONSES OF SETA TO FLUID MOTION

The transduction of a mechanical signal into electrical/chemical (neurophysiological) signals requires the mechanical opening of membrane bound ion channels. The short latency of the response argues against activation of a second-messenger cascade and favors direct activation of a mechanically sensitive channel [41]. Although the exact mechanism is still unknown, it is hypothesized [31] that the membrane bound channels are attached to rigid structures inside (microtubules) and outside (inner sheath cells) of the sensory cell *via* linking proteins (Figure 4). As the mechanoreceptive seta bend relative to the internal microtubules, the individual channels are pulled or stretched open allowing the influx of positively charged ions into the membrane. This influx creates the local depolarization which can lead to the generation of an action potential in the associated axon (*via* voltage gated ion channels; [42]). The frequency of the action potentials and the relative timing of firing between cells inform the broader nervous system of the direction and intensity of the external mechanical perturbation.

There are only a few studies aimed at quantifying the characteristics of setal motion that give rise to the neurophysiological response in copepods. Previous studies [56], which have used a vibrating bead as their stimulus, report that *G. princeps, Euchaeta rimana* and *Pleuromamma xiphias* can detect fluid displacement as low as 10-20 nm at corresponding fluid velocity of 20 to 40 $\mu m\ s^{-1}$.

However these values were based on calculated movements of the seta with the assumption that the seta accurately followed the movement of the surrounding fluid. Yen et al., [52] stimulated individual seta and found similar sensitivities for *Labidocera madurae*, with the sensitivity to displacement decreasing with decreasing stimulation frequency. To compare sensitivities of different seta it is helpful to normalize the data to individual setal length and report the displacement characteristics in terms of angular displacement and speed. Recalculating the data of Yen et al., [52], shows that at frequencies above 1000 Hz, the distal seta of *Labidocera madurae* have a displacement and velocity threshold of 10 nm and *ca.* 20 μm s^{-1}, respectively. For a setal length of 200 μm this is equivalent to an angular displacement of 0.003 degrees, and an angular velocity of 6 degrees s^{-1} (assuming maximum velocity is reached at half the oscillation cycle; [52]). This is extremely sensitive given that the smooth hairs of a crayfish are 3 orders of magnitude less sensitive [49].

At frequencies between 250 Hz and 1000 Hz the threshold displacement for *L. madurae* remained fairly constant at *ca.* 50 nm. This tip displacement corresponds to an angular displacement of 0.01 degrees and an angular velocity of 5-20 degrees s^{-1}. At frequencies more likely to occur in nature (< 200 Hz [57]; 10-50 Hz [19]) the threshold displacement required to elicit a neurological response varied inversely with frequency, with the seta becoming relatively insensitive, requiring larger displacements and velocities before a physiological response is initiated [52].

The data of Yen et al., [52] was extrapolated to more "natural" frequencies to predict that at 85 Hz and 10 Hz the 200 μm seta of *L. madurae* would require a displacement of 0.1 and 2.3 degrees, respectively, and corresponding angular velocities of 17.0 degrees s^{-1} and 41.4 degrees s^{-1}. At these lower frequencies the threshold values are up to 2 orders of magnitude greater for displacement and require a 3-fold increase in the angular velocity. This suggests that copepods may be significantly less sensitive to displacement and velocity at lower frequencies than previously assumed. However, these values are likely to be the realm of biologically relevant stimuli. Furthermore, if the displacement and velocity thresholds vary with frequency, they are not likely to be velocity or displacement sensors as much of the literature has concluded. Additional work in this area is certainly warranted.

NEUROLOGICAL CODING OF FLUID MOTION

When the motion of the setae surpasses the physiological threshold it generates a series of action potentials (Figure 6). Since the spike amplitude of an individual neurons is constant (see [58] for exception), information from a single sensory cell is provided by the timing of the first action potential, the length of time that the cell fires and the frequency at which it fires. Comparing the movement of the setae with the initiation of a spike train from a single neuron, we can determine the minimum displacement required to initiate the action potential in the associated neuron.

The length of time that the cell fires, provides information on the duration of the stimulus while the instantaneous frequency of the spike train, provides information about the intensity of the signal.

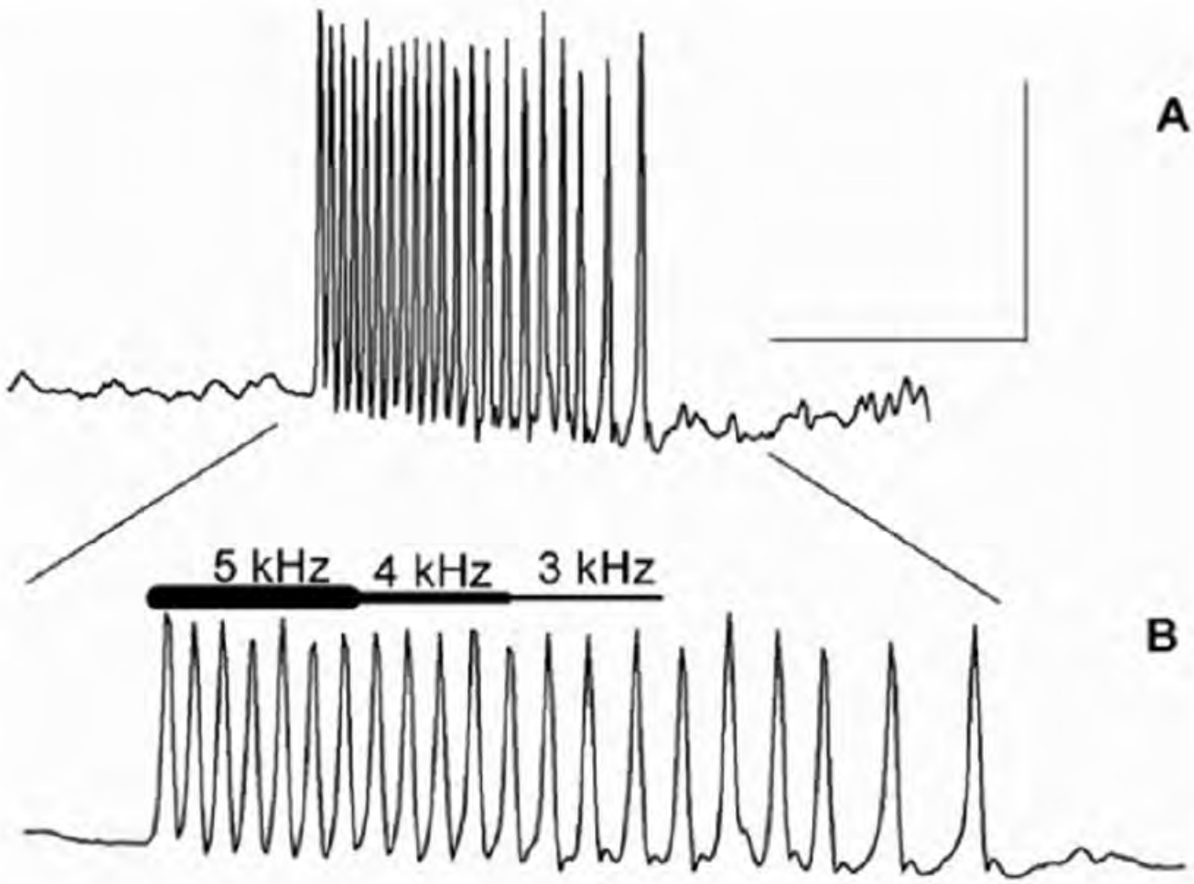

Figure 6. Neural recording from a seta of *G. princeps* (A) Series of the spikes recorded in response to a small water jet. Scale bar represents 500 μV on the ordinate and 5 ms on the abscissa. (B) Expanded view of the spike train. Note the high frequency response (3 kHz - 5 kHz) was sustained for over 3 ms. Modified from [42].

Rapid Behavioral Response

Detecting prey or avoiding predators is fundamental to the survival of individual copepods, and many animals derive a selective advantage by increasing their ability to rapidly evade predators or attack quickly moving prey. The pressure for rapid responses has led to special mechanical and neurophysiological solutions [59] to increase speed and diminish response time. Many of these solutions have evolved independently across different taxa [60]. The biological and physical environment of pelagic copepods requires highly discriminate and yet rapid behavioral responses. Living at low Reynolds numbers, chemical stimuli are transported to animal sensors largely through the slow process of laminar fluid displacement and Fickian diffusion [61]. Similarly, fluid mechanical stimuli are attenuated quickly by viscous dampening causing fluid velocity to decrease with distance cubed [11]. As such, copepods often do not detect other individuals until they are within a few body lengths of each other providing little time and information on which to base behavioral responses.

Responding in an ecologically appropriate manner with a 1 to 5 ms behavioral latency presents a unique challenge. Rapid and accurate behavioral responses of copepods require that three fundamental conditions be met. First, the neural impulses must have time to travel from the receptor site to the target motor region. Second, the neural impulses must contain adequate information to differentiate stimuli from each other and, third, they must provide

information to determine the 3-D location of the stimulus source. How does the neural system in copepods generate enough information in such a short time interval? Calanoid copepods possess numerous antennal sensors [22,29,30,35]. Depolarization of the nerve cell results from the deflection of the associated mechanosensory hair. Disturbance size is encoded by the number of setae simultaneously stimulated, whereas fluid velocity, at the level of the individual sensor, is encoded by the firing rate [62]. The rate and angle of deflection are likely to provide the animal with information regarding the velocity and potentially the acceleration of the fluid signal. Compared to other crustaceans [63], copepod mechanoreceptors are at least an order of magnitude more sensitive, which provides them with early detection of a potential predator allowing maximum time to collect information and initiate a behavioral response. To achieve both stimulus differentiation and behavioral latencies of 1 to 5 ms, individual neurons must fire at a minimum frequency of 250 to 1,000 Hz to generate the requisite 2-spike minimum to differentiate a signal from the spontaneous firing of a single action potential. Graded responses to fluid velocity, required for finer discrimination of signal strength, require higher frequencies. For example, coding a second or third magnitude of fluid velocity within the same 1-3 ms constraint would demand minimum frequencies of 2,000 and 3,000 Hz, respectively.

One mechanism to decrease the response time is to increase the rate that information travels along sensory neurons. For example, large diameter nerve fibers have evolved in numerous invertebrate species, such as the giant squid [64], crayfish [65], cockroaches [66] and older lineages of copepods [31]. Similarly, many vertebrates, and some more recent evolutionary lines of invertebrates such as copepods [67], have independently evolved myelin or myelin-like structures surrounding nerve cells to increase the speed of sensory or motor information. Doubling the speed, doubles the amount of information transferred during the same time period. Increasing the transfer of sensory information is analogous to an increase in "bus" speed in computer architecture. A second solution for moving sensory information quickly is by densely packaging information. Continuing with the computer analogy, this solution is analogous to increasing the size of the information packet (bit-size). By doubling the spike rate the transfer time decreases in half. Again it appears that copepods have evolved mechanisms to produce high frequency action potentials. Action potential frequencies in copepods can reach in excess of 5 kHz [42]. Little is known about the relationship between axonal conduction speeds and the action potential frequency and even less is known about the underlying mechanisms at the level of the ion channels within the nerves that permit such rapid firing rates. Further work in this area is hence certainly warranted.

DIRECTIONAL SENSITIVITY

Accurate attack and escape responses require not only detecting the magnitude of the stimulus but also its direction. In principle, direction can be discerned from a single seta housing multiple neurons that respond specifically to bending in certain directions. Anatomical observations of [33] for *Pleuromamma xiphias* suggest multiple innervation of some setae, but other studies found no physiological evidence of multiple innervation per seta [11]. However, significant asymmetry of the physiological response to proximal *vs.* distal deflections, in combination with directionally specific displacement-velocity curves can

produce stimulus-response functions that incorporated directional specificity. In some cases, morphological features on the antennule are key in producing these effects. For example, a cuticular socket that restricts motion of the seta in a particular direction [52,63,68] can provide a directional bias to the response [69]. Similarly morphological features of the setae can increase rigidity in one direction over another. Setae have been shown to have sharp angles located along the shaft, which offers increased rigidity when bent in one direction over another. Feathered setae are more responsive to flows contacting the brad face of the sensor rather than flows coming from the side. Similar results were found for insect hairs where the direction of best mobility accurately predicted the directional specificity of the neuronal response [70].

For copepods that have setae with single innervation it is unlikely that reliable directional signals can be garnered from the response of a single seta even with a mechanical directional bias. Since the activity of a single neuron depends on both the magnitude and the direction of the stimulus, different combinations of these two signal characteristics may lead to a similar neural response [71,72]. The signals from multiple setae, however, provide an excellent mechanism for spatial location. The temporal delay in firing between adjacent seta [35] can be used to both evaluate the speed of the disturbance and the direction. Increased fluid speed would decrease the lag time between the depolarization events and the order that the specific seta fire could distinguish the direction.

Mathematical Modeling of the Interaction between Medium Flow and Mechanosensory

Mathematical modeling has been employed to study the rather complex interaction between media flow (mostly air flow) and sensory hairs [43,71,73,74]; reviewed by Humphrey et al., [44,53]. The mechanics of stimulus coupling and transduction have been studied for numerous organisms including insects [73] and arachnids [44]. Tautz [73] was the first to suggest modeling the filiform hairs as forced damped harmonic oscillators to establish the dynamic characteristics of thoracal hairs in caterpillars. Typically the models have assumed the hairs to be smooth cylinders that respond as a stiff rod. Such simplified models seem to fit empirical data for many of the terrestrial organisms tested (although see Dechant et al., [45]. Humphrey et al., [48] provided an analytical mathematical-mechanical model describing the steady-state motion of a sensory hair protruding from a solid substrate in oscillating media (air or water) flows. Essentially, the hair is modeled as a rigid shaft with boundary conditions at the base. Using this model, Humphrey et al., [44] considered hair deflection for two biologically significant cases: (i) air flow oscillating parallel to the longitudinal axis of the spider leg (the substrate), and (ii) air flow oscillating perpendicular to the longitudinal axis of the spider leg. They found that the relative orientation between the respective directions of the fluid flow and the substrate axis has a significant effect on the magnitudes of hair deflection, angular velocity and acceleration but not on the resonance frequency of the hair. One potential problem of applying this model to copepods is that it calculated the displacement characteristics of the mechanosensory at resonant frequency. Copepods, because of their rapid behavioral responses, do not have time to respond to multiple cycles of an oscillating stimulus. Copepods can respond to fluid signals within 2 ms

of being generated. During this short time frame their seta would be exposed to only 1 complete cycle of a 500 Hz signal and only ½ a cycle for signals at 250 Hz [42]. This is insufficient to reach steady-state motion and the seta will certainly not achieve the same maximum displacements predicted at their resonant frequency. Rather than allowing the model seta to reach steady-state oscillations, using a modified Humphrey & Barth [48] model we consider only the initial displacement in a single direction. If the sensors are not allowed to reach steady-state (resonant frequency) the displacements are much smaller than analytical solutions would predict. Since copepods respond to fluid signals within milliseconds, the numerical model more accurately describes conditions experienced by the copepods and suggests that they must be much more sensitive to fluid motion (require much smaller displacement) than the analytical solutions would predict.

SPATIAL DETECTION OF FLUID SIGNALS

Positioned at the front of the copepod are two highly innervated antennae. For most pelagic copepods the antennae are a linear array of approximately 100 mechanoreceptive setae [50,52,75] that vary in length (Figures 7 and 8), thickness and orientation [76]. The individual setae on the antennule of the copepod are similar to the hairs cells of the human inner ear and the sensory cells within the lateral lines organ of fish. In all cases the mechanosensors serve as extremely sensitive mechano-electric transducers converting mechanical force into an electro-chemical signal. The signals are subsequently transmitted to the brain or peripheral ganglia where information from several sites may be integrated. One primary difference, however, is how complex signals that contain many superimposed frequencies and magnitudes are decomposed into their constituent properties. The human ear changes far field vibrations in the outer ear into a near field fluid disturbance in the inner ear. Within the inner ear, hair cells are arranged along the spiraling cochlea, which by virtue of its shape spatially separates the different frequencies such that they stimulate different sets of hair cells arranged along the length of the organ. The different clusters of hair cells are mapped in the brain to provide information on the narrow range in frequency that the spiral structure of the cochlea permits them to experience. In contrast, copepods do not have an external mechanism to spatial decompose fluid signals. The setae of copepods project directly into the fluid and are exposed to the entire symphony of frequencies. Thus for the animal to detect a wide range of signals with sufficient detail requires that individual hairs are be sensitive within a narrow range yet are adjacent to sensors that have complimentary tuning.

The antennules of copepods with a series of closely spaced flow sensors, provides an ideal structure for detecting fine scale heterogeneity in a local flow field (Figures 8 and 9). Setal morphology along the antennules of copepods and between species of copepods is highly diverse [30,33,77]. As discussed above, these differences in morphology allow copepods to detect a wide range of fluid characteristics at discrete locations along the antennules [35]. Encoding of spatial properties of a fluid disturbance, in contrast, occurs by comparing stimuli from numerous mechanoreceptive sites. Individual mechanosensors are arranged along the antennule much like an oceanographic deployment of a series of specifically tuned flow meters connected linearly along a single tether (Figure 9).

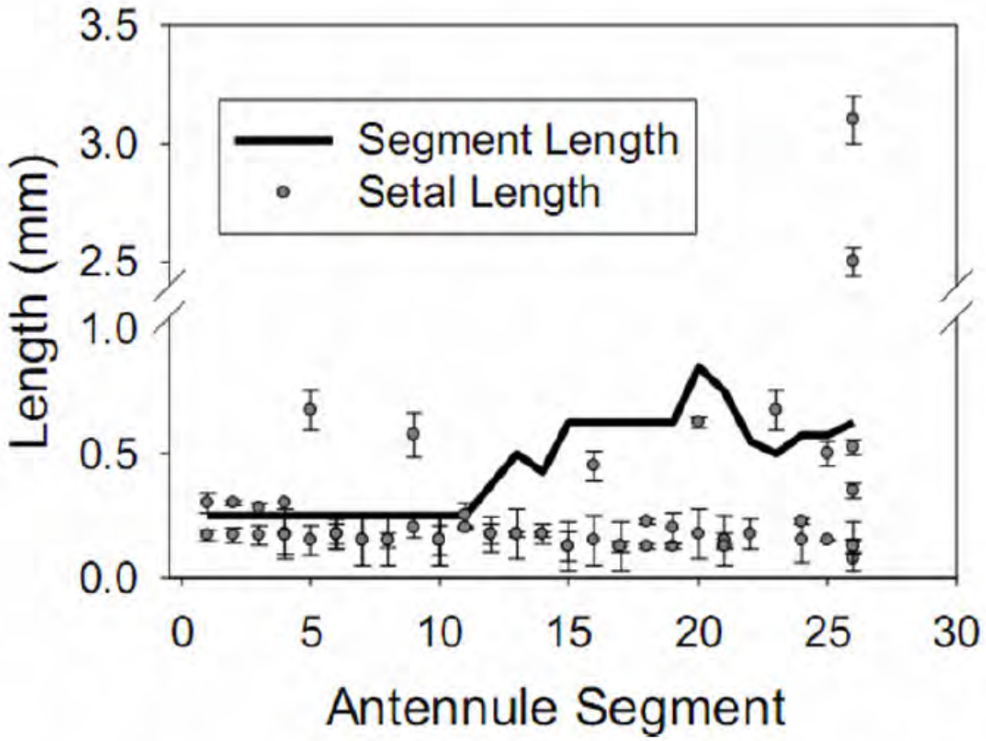

Figure 7. Antennule morphology of *Gaussia princeps*. Open circles represent the length of individual seta (±SE, $n = 6$). Solid line represents segment length. Note the very long mechanoreceptive setae on the final 2 segments of the antennule and the increase in segment length at segment 11-26.

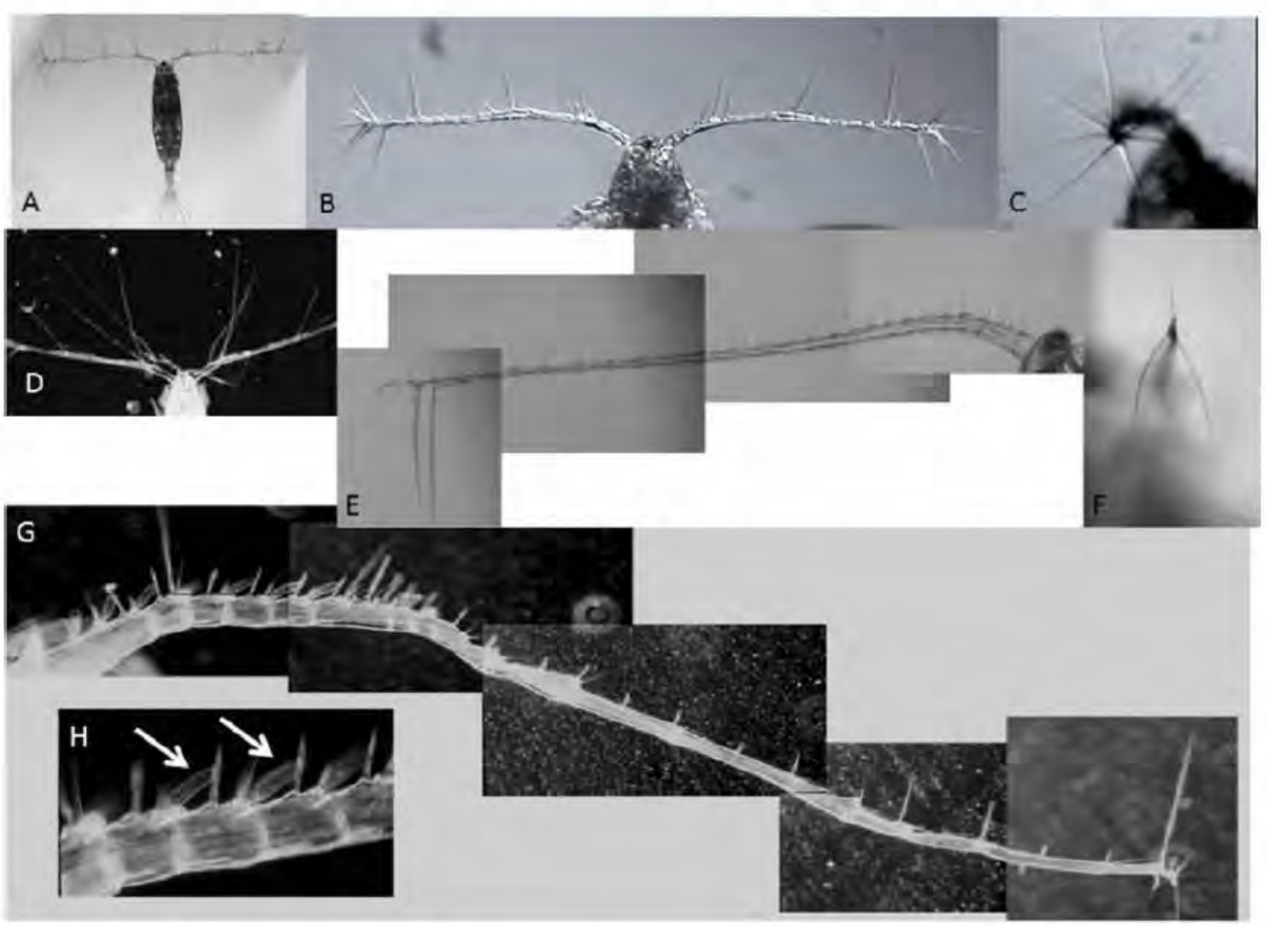

Figure 8. Antenules of different copepod species. *Acartia tonsa* (940 µm) dorsal (A-B) and lateral view (C). Oithona sp. (D). Calanus *finmarchicus dorsal* (E) and lateral view (F). *Pleuromamma* xiphias (4.2 mm) male right antennule (G-H). Arrows mark putative chemoreceptors.

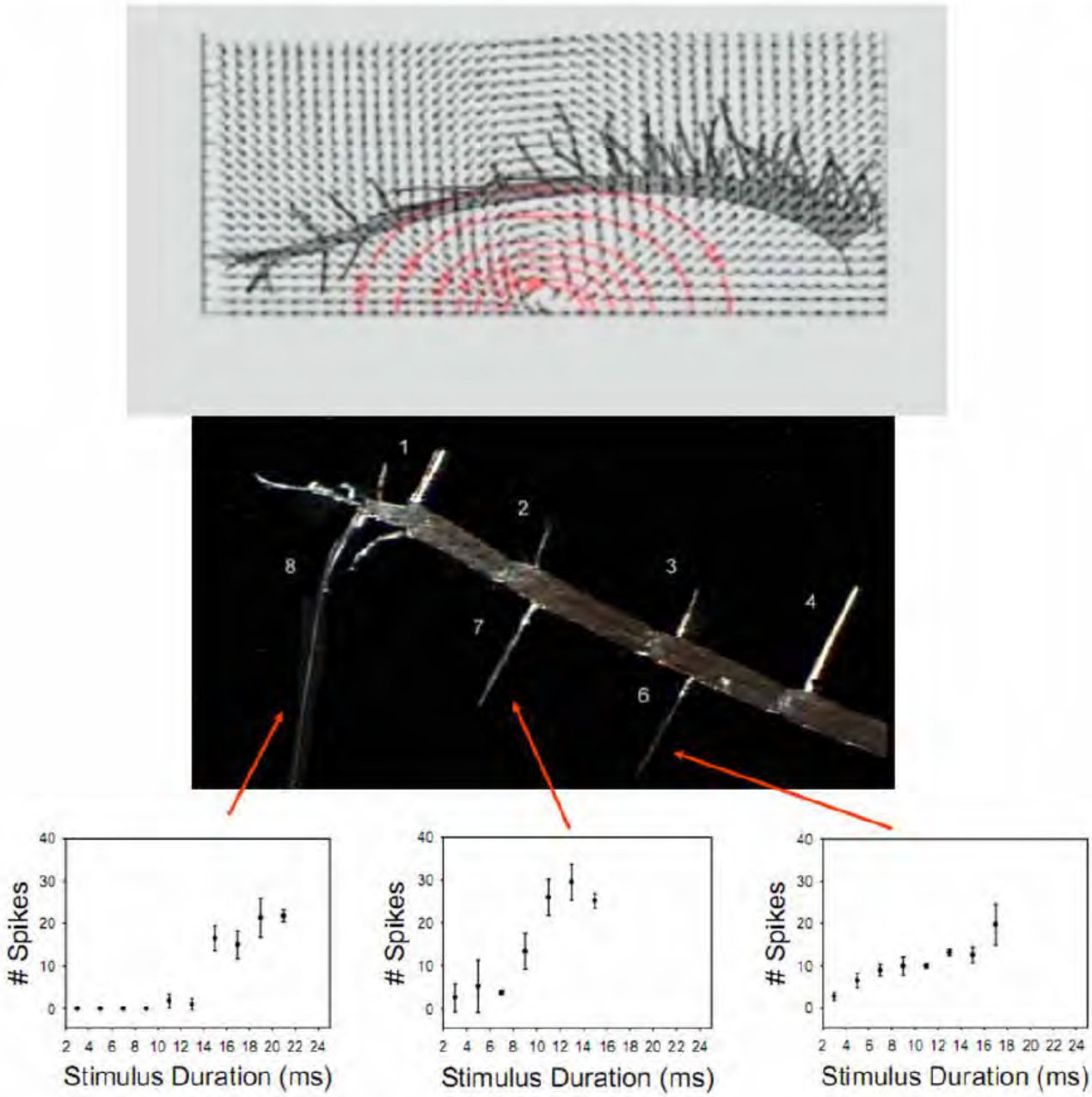

Figure 9. Upper panel: a schematic (based on real data) of the antennule of *Eurytemora* sp. made from light and SEM images (Fields, unpublished data) superimposed on a CFD solution for a copepod jumping [24]. Arrows represent magnitude of fluid motion. Note that each seta is exposed to a different (time dependent) fluid intensity. Lower panel: neurophysiology as a function of signal strength for 3 different setae on the antennae of *G. princeps*. Each seta has different physical characteristics, response profile and directional sensitivities (not shown).

Sensors are densely packed in regions where measurements of fine scale structure are needed, and distributed over a greater distance when their task is the detection of larger spatial features. A long antennule span provides greater spatial coverage, but decreases resolution of finer scale features, assuming a constant number of sensors. Behavioral responses of copepods to fluid motion suggest that they detect spatial gradients in fluid velocity [14]. Copepods often are smaller than the smallest turbulent eddies in their environment [78,79] and frequently experience fluid disturbances as 3-D laminar shear. Directional sensitivity of individual setae and their linear distribution along the antennule suggest that detection of velocity gradients is maximized within the plane defined by the body and the antennules [80]. Thus the relative orientation of the copepod within a larger

hydrodynamic feature will determine its ability to detect the surrounding flow. If individual setae all have the same sensitivity, the length of the antennule would determine the maximum distance over which a given velocity gradient is detected (Figure 10). Small increases in antennule length give rise to a large difference in the velocities at either end of the antennule, since fluid velocity decays exponentially with distance.

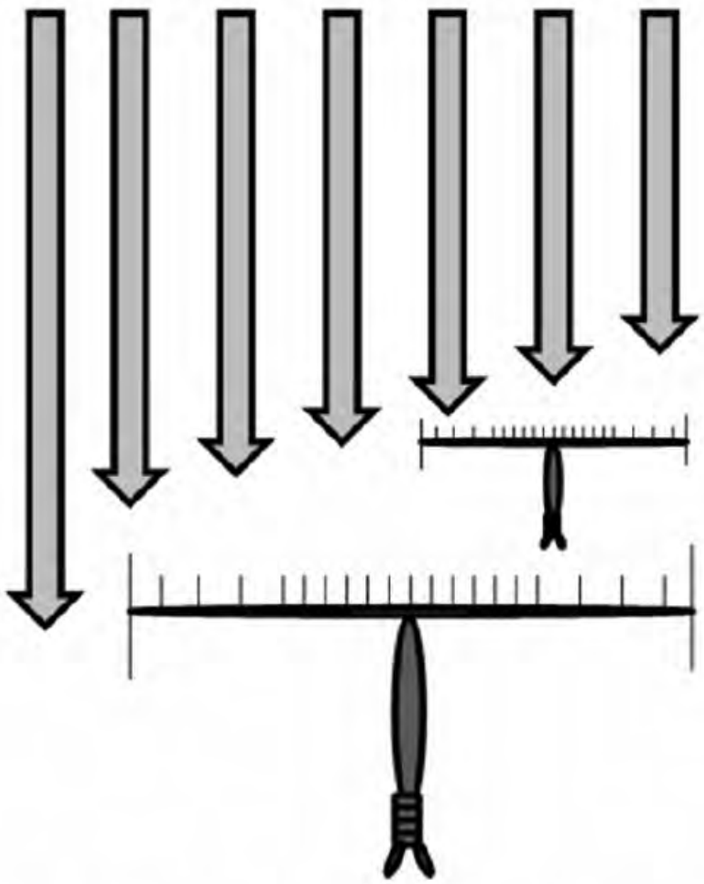

Figure 10. Two copepods with different antennule lengths exposed to the same fluid disturbance. The copepod with the short antennules cannot detect the small gradient in fluid velocity while the animal with the large antennule span detects the spatial difference in fluid speed.

For example, Yen et al., [52] reported a velocity threshold of 20 μms^{-1} for an individual mechanosensor. If we assume that this threshold remains constant, an animal with a 1 mm antennal span can potentially detect a sheared flow of 0.02 s^{-1}. In contrast, an animal with a 5 mm antennal span and the same sensitivity could detect a shear of 0.006 s^{-1}. These shear levels would be created under an isotropic turbulence level (ε) of 0.5 and 0.04 $cm^2\ s^{-3}$, respectively [81]. Thus, the two hypothetical animals would be expected to have an order of magnitude difference in sensitivity to the same velocity gradient, despite equal sensitivity of the individual mechanosensors. A long antennule with a high sensitivity to velocity gradients benefits animals that live in the relatively quiescent environment of the deep ocean, but it could make them overly sensitive to ambient hydrodynamic disturbances in the upper water column. Since copepods must balance the risk of predation with the energetic cost of an unnecessary escape [14], acute sensitivity to shear may be disadvantageous where ambient turbulence is large. The trade-offs inherent in antennule architecture may result in correlations between morphology and turbulence level preferred by a copepod species. Since copepod species of similar size can have antennal spans that differ by 25 to 30% [82], knowledge of

how copepod species are distributed may provide a quick and reliable measure of the instantaneous oceanic turbulence, particularly if distributions reflect active choices made by animals.

Behavioral assays quantifying the escape threshold of different developmental stages of a single species, *Acartia tonsa,* show a similar size-dependency [76] as behavioral sensitivity is markedly enhanced by increased antennule length [14,15]. This change in sensitivity does not appear to be the result of changes in the sensitivity of the individual mechanoreceptor. Boxshall et al., [83] suggested that sensory structures responsible for predator detection (namely the distal tips of the antennules) appear early in development and are conserved throughout ontogeny. Individual antennule segments lengthen as animals develop through the copepodid stages to adulthood. This gives rise to an increase in the overall length of the antennule with little change in morphology at the distal tips. Thus the inverse relationship between antennule size and escape threshold suggests that the mechanism underlying the higher predation risk of nauplii may be their decreased sensitivity to fluid signals created by potential predators.

THE ROLE OF FLUID VISCOSITY ON MECHANORECEPTION

Environmental conditions play a primary role in the transmission of sensory signals. Changes in the physical characteristics of the fluid can alter the detection distance and signal structure. For example, temperature is inversely correlated with kinematic viscosity of fluids. Animals in the tropics and regions surrounding the Mediterranean Sea experience viscosity values that are approximately 50% of those found in the polar region. The resonant frequency of an individual mechanoreceptor varies inversely with kinematic viscosity [48]. Similarly, the maximum displacement at its resonant frequency increases with the cube of viscosity. Thus mechanoreceptors of a polar copepod (living at -1°C) with a resonance frequency of 100 Hz would experience a shift in the frequency of maximum response to 200 Hz in equatorial regions (25°C). Furthermore, the maximum displacement of the seta at its resonant frequency decreases exponentially with viscosity, giving the equatorial copepods a maximum displacement that is $1/8^{th}$ of that in the polar copepod. This makes individual setae in the equatorial region much less sensitive to a given fluid speed. Under an assumption of constant frequency sensitivity, to maintain the same maximum displacement, equatorial animals would need to increase setal length by a factor of 4. However, in tropical and Antarctic congeners of *Euchaeta* (*E. rimana* and *E. antarctica*) setal length from segments 3, 7, 13 decrease (rather than increasing) by a factor of 1.8 to 2.0 (data from Yen & Nicoll [32]). Similar results are found for tropical and subpolar *Acartia* congeners (*A. tonsa,* living at 22°C, and *A. tumida*, at 3°C). This suggests that congeners living in different viscous regimes do not dynamically scale (to compensate for viscosity) the length of their seta to maintain spectral sensitivity. Instead, copepods may be regulating the size of their perceptive field. Higher viscosity (colder temperatures) increases the rate at which an initial disturbance is dampened; fluid mechanical signals in warm water maintain their velocity over a greater distance than in cold water. Thus, polar animals must have long setae that respond at lower signal amplitude in order to effectively perceive prey from a distance. This same level of sensitivity would increase the perceptive field of tropical copepods well beyond its ecologically relevant space.

The perceptive field must be large enough to allow an appropriate response, but not so large that it includes excessive sensory information. Signals emanating from a large distance may be so far away that they are irrelevant to an animal ability to effectively capture a prey or escape predators. As a result, copepods that live in low viscosity environments, where fluid signals travel much further, may have shorter setae to diminish their perceptive field.

SUMMARY

The ability to sense fluid motion is strongly influenced by morphological properties of setae, by the way in which they are organized into an ensemble along the mechanosensory organ (i.e., the antennule) and the physical charicteristics of the fluid in which they are embedded. Setal length and orientation affect how they encode basic properties such as velocity, frequency and direction, whereas the arraignment of setae along the body and antennules mediate perception of more complicated properties, such as shear. Morphological and physiological data indicate that the design of setae and antennules bias an organism towards detecting particular types of disturbances, or for efficient operation in certain environments. These structure–function relationships provide potential insight into the diets and the dominant predators of different copepod species and perhaps can explain the tremendous degree of variation in setal morphology and antennule architecture. However, structure–function predictions are premature because we generally lack complimentary data on both the design and ecological roles of the mechanosensory system in a particular organism. Thus, an important challenge is to use a comparative approach to determine whether design principles of mechanosensory systems can explain behavioral properties, and therefore provide insights into ecological interactions in the plankton.

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