

Pain in fishes: The extent to which fishes can perceive noxious stimuli and experience pain is a central issue in the development of animal welfare practices for species being farmed under intensive conditions (reviewed in Chandroo et al. 2004). Techniques from the sensory biology toolbox—neuroanatomy and electrophysiology—have recently been applied to address these questions (Sneddon et al. 2003, Sneddon 2004). These authors conclude that there is a neuroanatomical and physiological basis for pain perception in fishes, and that a sense of pain is evolutionarily old and conserved. Although this view is not universally shared (e.g. Rose 2002), if it is substantiated it will have broad implications for animal welfare practices in farmed fishes.

In closing. We must always keep in mind that every complex organism is linked to its ecology through its perception of the world around it. Hopefully, the examples presented above, and elsewhere in this TS, will sensitize readers to the importance of sensory biology in establishing the mechanistic basis for this connection.

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Evolutionary and ecological significance of mechanosensor morphology: copepods as a model system

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Organisms must detect and respond to environmental and biological cues to behave in an ecologically appropriate manner. Implementing these behaviors requires that organisms derive environmental information from activity of their sensory neurons, with each individual receptor acting as a broadband filter for biologically relevant signal properties. As a result, the suite of potential signals is determined by characteristics of individual sensors and the architecture of the entire sensory system. For example, the composition of visual pigments within the eye fundamentally controls the light spectrum to which an animal can respond.

Photopigments absorb only certain wavelengths, and so the range of perceivable colors depends on the variety of pigments contained in the population of receptor neurons (Lythgoe 1979). Similarly, the molecular specificity of individual chemoreceptors, in conjunction with the diversity of receptor types, determines the chemical signals available to an organism (Derby & Atema 1988). 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. 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. Our focus is on planktonic copepods as model organisms for studying the role of mechanoreception because: (1) they are a critical component of aquatic environments; (2) fluid signals often act as the final proximate cue for copepod behavioral responses; (3) the basic properties of the copepod mechanosensory system are relatively easy to identify, and may be broadly general across a diverse range of species.

Copepods commonly show a graded response to purely fluid mechanical signals (Drenner & McComas 1980, Fields & Yen 1997, 2002, Kiørboe et al. 1999). Preliminary evidence suggests that behavioral patterns are evoked in response to relatively few neural signals (Fields & Weissburg 2004) that emanate from sensory setae adorning the antennule (Yen et al. 1992, Fields et al. 2002). Previous work has identified behavioral thresholds and examined the underlying processes involved in the transduction of fluid motion to neurological signal (Yen et al. 1992, Fields & Yen 1997, Fields et al. 2002, Fields & Weissburg 2004). Although it is likely that chemicals and light play a regulatory role in modulating behavioral thresholds, the proximal cue eliciting predatory, escape or mating responses typically is a fluid mechanical disturbance. The structure and function of copepod mechanosensors likely 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 antennule and setal morphologies, orientations and degree of ornamentation (Huys & Boxshall 1991). 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. Modeling studies of fluid–mechanosensor interactions (Humphrey et al. 2001) and our own empirical data on physiological response of mechanosensors suggest how copepod mechanosensory systems may be tuned for specific properties via their particular morphologies. The potential ease of using morphological traits as opposed to behavior or gut analysis provides a potentially powerful tool for quickly characterizing different feeding guilds and oceanic environments, including difficult to sample microenvironments. As such, key sensory architectures can provide an index into present day conditions or offer insight into paleo-conditions (Marcotte 1999). For sensory biology to generate ecological insights, a firm understanding of sensory mechanisms must be coupled to information on spatial and temporal distributions of animals in relation to the sensory environment. Only recently have we come to understand enough about mechanosensation in the plankton to suggest key features of sensors that determine animal abilities. The novelty of this approach, combined with difficulties in observing plankton behavior or mapping plankton distributions to relevant environmental parameters (e.g. turbulence; see below), means that we are unable to advance firm conclusions. Rather, we offer speculations and predictions that are well grounded in our analysis of sensory mechanisms, but which can be verified only with further ecological and behavioral evidence.

From fluid motion to mechanoreception. The individual mechanoreceptor: Copepods must feed, avoid predators, and find mates. Our working hypothesis is that 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) faced by a given organism. Thus, it is imperative that we characterize, in a mechanistic way, how sensors respond to quantified, biologically relevant fluid disturbances to fully appreciate what the sensor morphology reveals about the environment and ecological pressures faced by these animals.

Mechanoreception provides the shortest latencies in neural signal transduction because of the direct coupling between sensory hairs and the actual ion channels. To initiate a neurophysiological response, mechanoreceptors require a minimum critical displacement. Once the seta surpasses the minimum displacement threshold, the firing rate of the associated neuron correlates to the first or second derivative of displacement with respect to time (velocity or acceleration receptors; D. M. Fields & M. J. Weissburg unpubl.). Copepods require 0.1 to 2.3° of angular displacement (Yen et al. 1992, D. M. Fields & M. J. Weissburg unpubl.) to initiate a neuronal spike. Achieving threshold displacement depends on the velocity of the

fluid (amplitude) and the duration of the pulse (frequency). Mechanoreceptive hairs in water oscillate at the frequency of the surrounding media with a characteristic resonance frequency (ω_{res}) that varies inversely with the length of the seta (L) cubed,

$$\omega_{\text{res}} \sim L^{-3} \quad (1)$$

and inversely with fluid viscosity (μ)

$$\omega_{\text{res}} \sim \mu^{-1} \quad (2)$$

At its resonance frequency, the maximum displacement (θ_{max}) is directly proportional to the length of the seta (L) to the power of 1.5,

$$\theta_{\text{max}} \sim L^{1.5} \quad (3)$$

and directly proportional to viscosity cubed,

$$\theta_{\text{max}} \sim \mu^3 \quad (4)$$

(Humphrey et al. 2001). From these relationships, several simple conclusions can be drawn concerning both the length of the seta used to detect particular frequencies and the relative sensitivity of specific setae in different fluid environments. (1) Long setae show their maximum response at a much lower frequency than do short hairs; further, since ω_{res} is proportional to L^{-3} , small decreases in setal length give rise to large changes in the optimal frequency. (2) Long setae require greater linear displacements to reach the critical 0.1 to 2.3° needed for a neural response; this greater distance, coupled with the slower speed of displacement at the optimal frequency, lead to a longer response time for longer seta. Since rapid responses are critical to the survival of copepods (Fields & Weissburg 2004) the use of long setae may be constrained to gathering information for behavioral responses that are relatively less time sensitive. (3) Long setae at their resonant frequency reach a greater maximum angular displacement than short setae at the same stimulus amplitude. This allows longer seta to be more sensitive to smaller amplitudes than short setae, but demands that the stimulus operates over a long time period.

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; Alcaraz & Strickler 1988, Fields & Yen 2002), should be adorned with short setae. In contrast, copepods will have longer setae if they must detect slow moving, low frequency disturbances, because detection of these signals will require sensitivity to very small fluid displacements. The optimal length must 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 com-

plement 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 as soon as fast moving prey are within the capture region. The signals produced here 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.

Sensory morphology and feeding mode: Although the morphology of the mechanoreceptors is likely constrained by factors not pertaining to sensory perception, several examples clearly illustrate the associations between sensor length and complement, and diet. Predators from the genera *Candacia*, *Euchaeta*, *Gaussia*, *Oithona* and *Pleuromamma*, all have a few long setae (750 μm and longer) interspersed with numerous shorter ones within the proximal region of the antennules (Landry & Fagerness 1998, Paffenhöfer 1998). This arrangement implies a relatively large perceptual space combined with the ability to detect prey attempting to escape from the capture area. In contrast, herbivores or facultative carnivores (which prey on relatively slow moving animals) such as those in the genera *Calanus*, *Centropages* and *Labidocera* lack long setae in the proximal region. The predominance of shorter setae suggests a bias towards close range perception, because a weak swimmer will not generate sufficient disturbance to be detectable unless it is within the capture volume.

Gender differences in species that have non-feeding males, such as *Euchaeta rimana*, show a pattern in setal morphology similar to that seen in predators vs. herbivores. The feeding females have long setae, while the non-feeding males do not. Interesting, however, are species where the males continue to feed, but show pronounced morphological differences in setae along their antennules. For example, *Pleuromamma xiphias* females have 3 long setae within the first 13 segments of the antennules and consume highly motile prey with acute mechanosensory abilities. Prior to their final molt to adulthood, the antennules of males display the same morphology as those of females. However, the antennules of reproductively viable adult males become geniculated, gain numerous chemosensors and lose the long mechanosensory seta on Segment 13. Comparisons of male and female feeding behavior show decreased ability of the adult males to capture rapidly escaping prey (D. M. Fields unpubl.).

The long setae, with their high sensitivity to small displacements, support maximum detection distance. Thus, on the basis of these observations, it is tempting, but unfortunately premature to suggest that detection distance and degree of carnivory are positively correlated with increased setal length, particularly in the proximal segments. However, a more systematic and complete survey of both the diet and the setal morphology of copepods may allow us to predict the trophic status based on the appearance of their sensory hairs. Although the morphology of sensors in the proximal region seems variable across different genera, the distal segments of most pelagic copepods are fairly conserved and typically have the longest seta of the entire antennule. The greatest spatial information is obtained by comparing fluid velocity information gathered from the distal tips of the antennule. As such, this region, as a result of its greater spatial sampling, has been suggested to be the location for predator detection (Yen et al. 1992). Long distal setae seem to be an ancestral condition in copepod lineages (Huys & Boxshall 1991), suggesting that predator avoidance may have been a major factor driving the structure of the copepod mechanosensory system.

Setal morphology will also affect the geometry of a predator's perceptual space. Setae are not equally compliant in all directions, and this results in variation in both setal motion and neurophysiological response to water motion applied from different locations (Fields et al. 2004 and references therein). Interestingly, the highly predatory copepods discussed above also have setae aligned both parallel, and off-axis, to the plane defined by the antennule (Landry & Fagerness 1988, Yen & Nicoll 1990). These array designs may facilitate prey perception in larger water volumes. *Euchaeta* spp. has a 3D capture volume (Doall et al. 2002), but the perceptual spaces of other carnivorous copepods remain unknown. As demonstrated by the ongoing discussion of turbulence vs. predation intensity (Browman & Skiftesvik 1996), it is essential to understand the geometry of a predator's perceptual space in order to fully examine the impacts of environmental variation on predator-prey relationships.

The ability of sensors to detect specific fluid structures may play a role in the vertical distribution of different copepod species and developmental stages (Mackas et al. 1993). Copepods with highly sensitive mechanoreceptors (large perceptive field) can efficiently detect food at a distance if the background turbulent energy is relatively low, and consequently may be able to occupy quiescent regions of the water column with low food levels. However, excess hydrodynamic noise caused by turbulence, internal waves, or other highly sheared flows can interfere with the detection of pertinent signals, and these same animals

might not be as competitive in highly turbulent regions where their perceptive field is severely diminished. These tradeoffs in sensor response properties suggest that specific sensory architectures permit copepods to exploit particular resources and/or constrain them from exploiting others. However, it is technically challenging to map copepod distributions onto patterns of fine-scale turbulence, and such efforts are few. Consequently, although copepod species have been seen in regions characterized by particular turbulence levels (e.g. Mackas et al. 1993), the mechanisms that underlie these patterns are unclear. Copepod species may seek out regimes in which they perform optimally, or their distributions may be driven by purely physical mechanisms (e.g. Haury et al. 1990). Thus, mechanosensory abilities may explain why copepods prefer certain environments, and may thus predict their distributions, or alternatively provide hypotheses regarding the persistence of local populations transported into particular regimes.

Antennules as detectors of spatial structure. Copepod antennules are a linear array of less than 100 setal mechanosensors orientated at discrete angles along the antennules (Huys & Boxshall 1991, Kurbjewit & Buchholtz 1991, Yen et al. 1992, Fields et al. 2002). Each seta is typically innervated by 1 to 2 neurons (Weatherby et al. 1994, Fields et al. 2002). The antennule of the ancestral female copepod consists of 28 segments, numbered from proximal to distal. Modification in the pattern of setation and fusion of the segments over evolutionary time provides important taxonomic characteristics and allows rapid discrimination of gender (Huys & Boxshall 1991). Yet, little work has been done to explore geographical or feeding guild patterns of different antennule morphologies, or the

selective pressures that drive evolution of different morphologies. As discussed above, the morphology of the antennules and of the associated setae dictates the stimuli that the animals can detect, providing a potential link between antennular morphology and organismal abilities.

The general structure of the antennule suggests how antennular morphology affects perceptive abilities. The proximal segments of the antennules are significantly shorter than the distal segments in most pelagic copepods (Huys & Boxshall 1991; e.g. Fig. 1). The number of sensors generally is constant despite changes in segment length. We have previously suggested that regional differences in sensory architecture reflect the sensory tasks handled at the different locations of the antennule. The proximal region controls feeding and mate detection, and the distal region is used mostly for predator avoidance. The neurological responses of individual setae encode fluid velocity, acceleration and duration of the disturbance (Fields et al. 2002, Fields & Weissburg 2004), and are contingent upon the physical characteristics of the mechanoreceptive hair and its coupling to the cuticle. Setal morphology is highly diverse (e.g. Friedman & Strickler 1975, Bundy & Paffenhöfer 1993, Weatherby et al. 1994) and, as discussed above, these differences are fundamental to the animal's ability to detect a wide range of fluid characteristics (Fields et al. 2002). Encoding of spatial properties, in contrast, occurs by comparing stimuli from numerous mechanoreceptive sites. A greater antennule span provides a larger perceptive field, but decreases resolution of finer scale features, assuming a constant number of sensors. Thus the 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. Sensors are densely packed in regions where fine scale structure is needed, and distributed over a greater distance when their task is the detection of larger spatial features.

Spatial detection and antennule design. Behavioral responses of copepods to fluid motion suggest that they detect spatial gradients in fluid velocity (Fields & Yen 1996, 1997). Copepods often are smaller than the smallest turbulent eddies in their environment (Fields 1996, Webster et al. 2004) and frequently experience fluid deformation as laminar shear. Although there is no consensus on the appropriate unit of measurement for quantifying the fluid characteristics relevant to copepod behavior (i.e. shear strain vs. linear shear; see Kiørboe et al. 1999, Fields & Yen 1997), setal directional sensitivity and anatomy (setae are positioned as a linear array along the antennule) show that the ability to detect velocity gradients is biased in favor of detection within the plane defined by the

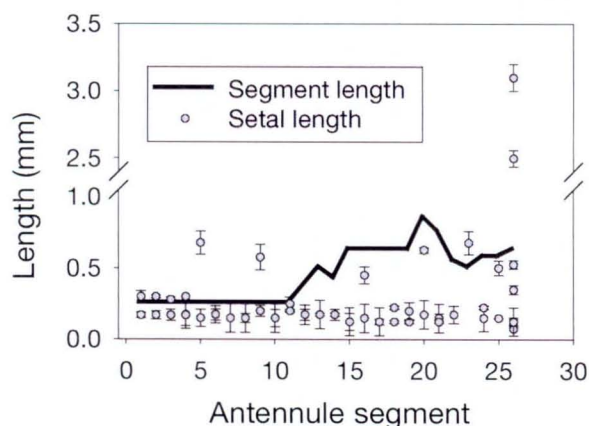


Fig. 1. *Gaussia princeps*. Antennule morphology. Dots represent setal length of individual hairs (\pm SE, $n = 6$). Solid line shows segment length. Note the increase in length at segment 11

body and the antennules. Thus the relative orientation of the copepod within a larger hydrodynamic feature will determine its ability to detect the surrounding flow. Assuming setae all have the same sensitivity, the length of the antennule will determine the distance over which a velocity gradient is detected. Small increases in antennule length give rise to a large difference in the velocities detected at either end of the antennule, since fluid velocity decays exponentially with distance. For example, Yen et al. (1992) reported a velocity threshold of $20 \mu\text{m s}^{-1}$ 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 $0.04 \text{ cm}^2 \text{ s}^{-3}$, respectively (Hill et al. 1992). Thus, the 2 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 (Fields & Yen 1997), 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% (Paffenhöfer 1998), 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 (Fig. 2), as behavioral sensitivity is markedly enhanced by increased antennule length (Fields & Yen 1997, Kjørboe et al. 1999). This change in sensitivity does not appear to be the result of changes in the sensitivity of the individual mechanoreceptor. Boxshall et al. (1997) 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 viscosity. Temperature has a strong effect on kinematic viscosity. Animals in the tropics and regions surrounding the Mediterranean Sea experience viscosity values that are approximately 50% of those found in the polar region. Increased viscosity alters the perceptual ability of Antarctic copepods (Mellard et al. 2005, Yen et al. 2005) and affects the underlying workings of their small sensory structures. For example, the resonant frequency of an individual mechanoreceptor varies inversely with kinematic viscosity (Eq. 2). 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 (Eq. 4), giving the equatorial copepods a maximum displacement that is 1/8th of that in the polar copepod. This makes the individuals in the equatorial region much less sensitive to a given fluid speed. Under an assumption of constant frequency sensitivity animals in the equatorial regions should increase setal length by 25%. To maintain a constant 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 decreases (rather than increasing) by a factor of 1.8 to 2.0 (data from Yen & Nicoll 1990). Similar results are found for tropical and

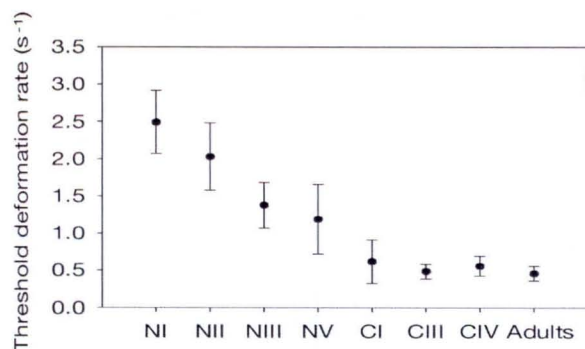


Fig. 2. *Acartia tonsa*. Escape threshold ($\pm 95\%$ CI) of developmental stages from a siphon flow (Redrawn from Kjørboe et al. 1999)

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 as to be irrelevant to an animal's ability to effectively capture a prey or escape predators. As a result, copepods that live in low viscosity environments, where fluid signals travel much farther, may have shorter setae to scale down their perceptive field.

Summary. The ability to sense fluid motion is strongly influenced by morphological properties of setae and by the way in which they are organized into an ensemble along the mechanosensory organ (i.e. the antennule). Setal length and orientation affect how setae encode basic properties such as velocity, frequency and direction, whereas the arraignment of setae 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 trophic status, predator detection abilities or distributions, and perhaps can explain the fantastic degree of variation in setal morphology. However, structure–function predictions remain largely unverified, because we generally lack complementary 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 organismal properties, and therefore provide insights into ecological interactions in the plankton.

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Animals as prey: perceptual limitations and behavioural options

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Perceptual abilities and predation risk. Animals are under constant pressure to rapidly sort, assess and act upon the stream of sensory signals they receive from the environment. The resulting actions form the basis of how organisms respond to each other and to the world around them. However, information processing takes time and sensory systems have limitations. As a consequence, animals are rarely in a position to make fully informed decisions. For example, when first becoming aware of a predator, potential prey may not be able to tell exactly how far away the threat is, or how fast and in which direction it is moving, because of limitations on the range and accuracy over which animals can measure an object's distance (e.g. Collett & Harkness 1982). In many situations, animals cannot afford to wait to gather reliable information before deciding to take evasive action. Prey animals must deal with such uncertainty in ways that are both safe and minimize false alarms. The perceptual limitations of animals thus affect their ability to assess current risk and their options to respond (e.g. Fernández-Juricic et al. 2004) with far-reaching consequences for their lifestyle (Lima 1998) and for the distribution and the dynamics of populations (Luttbeg & Schmitz 2000). In theoretical work, the problem of limited information is dealt with by asking how the 'value' and the 'reliability' of available information affect decision making strategies (e.g. Welton 2003, Koops 2004 and references therein). However, in most cases, the sensory abilities of animals and their behavioural options are unknown, so that we must make assumptions on how animals assess risk and how this assessment affects the decision making process. Despite extensive field and laboratory research (e.g. Curio 1993, Fernández-Juricic et al. 2004), we are still unable to explain how the 'quality of information', i.e. the correlation strength between sensory cues and actual threat, influences prey anti-predator responses on a moment to moment basis. The chief difficulty is that it has been impossible to measure, in a natural situation, the stream of predator-related sensory signals and their value for current risk assessment, together with the defensive behaviour of prey animals.

Measuring sensory information and behaviour. We reason that the clue to understanding predator–prey interactions lies in the details of perceptual capacities