

Applications of sensory biology in marine ecology and aquaculture

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Sensory perception links an organism's internal and external ecologies. It thereby also connects conspecifics to one another, and underlies many of the biological–ecological links between species in communities. My goal here is to demonstrate how studying these perceptual links can help marine ecologists and aquaculturists understand the basis for the responses (or lack thereof) that they observe in the field, the laboratory, or the culture tank. The case studies that follow were chosen to underscore that some processes in marine ecology and aquaculture can only be addressed through the eyes (and/or other senses) of the organism(s) involved. In each case, I emphasize how the answers that issue from such an approach can be of great practical advantage.

Applications in marine ecology. Turbulence and predator–prey interactions in the plankton: Substantial effort has been applied to demonstrate that microscale turbulence can significantly increase the feeding rate of planktonic predators (reviewed in Dower et al. 1997). This effort has been driven by the theoretical conclusion that microscale turbulence increases the encounter rate between planktonic predators and their prey. The original theory assumed that the geometry of the water volume perceived (i.e. searched for prey) by a predator is spherical (Rothschild & Osborn 1988). More recent theoretical formulations assume a forward-projecting hemispherical perceptual volume (reviewed in Dower et al. 1997, Galbraith et al. 2004). However, for all planktonic taxa for which such information exists, the geometry of the perceptual field is neither a sphere nor a hemisphere (see Lewis 2003, Galbraith et al. 2004). The manner in which a non-symmetrical perceptual field might affect the conclusions of turbulence encounter theory was recently examined by Lewis (2003) for cruise searching copepods. He concludes that under turbulent conditions the optimal swimming strategy (associated with prey search) for predators with non-symmetrical perceptual fields differs radically from what is otherwise predicted. Analogous work on larvae of Atlantic cod *Gadus morhua* produced a similar result: the advantage of turbulence is greatly reduced when the perceptual space is parameterized with a more realistic geometry (Galbraith et al. 2004). Since virtually all models of predator–prey interactions in the plankton—zooplankton–phytoplankton; zooplankton–zooplankton; ichthyoplankton–zooplankton—are based upon a

parameter for the distance at which prey can be located, this demonstrates how empirical knowledge of the perceptual abilities of marine organisms is essential. Without such information, we risk making large errors in prediction, which can lead to misleading and/or incorrect conclusions.

'Operational' prey abundance and the myth of prey choice/prey selectivity by small zooplanktivores: Although the abundance of prey that could be consumed by small zooplanktivores is temporally and spatially highly variable, it most often ranges between 0 and 10 l^{-1} . The volume of water contained in the visual perceptual field (VPF) of a 6 to 10 mm fish larva is approximately 0.8 to 1.0 ml (see Browman & Skiftesvik 1996, Galbraith et al. 2004). Thus, at an *absolute* prey abundance (AA) of 100 l^{-1} , there would be only 0.08 to 0.1 prey items within the VPF at any given instant. The number of prey per VPF is the *visual* abundance (VA); from the perceptual perspective of the predator, VA, *not* AA, is the operational measure of prey availability. Thus, for this fish larva, AA would have to be $>2000\text{ l}^{-1}$ in order for VA to be >1 (prey aggregations at thin boundary layers may be this dense: Gallager et al. 2004). This example illustrates that small zooplanktivores—e.g., carnivorous copepods or fish larvae—will rarely have an opportunity to *actively* choose from amongst several simultaneously available prey items. While it is possible that these predators make choices from amongst prey encountered sequentially, under anything but the highest of prey abundances, they must eat whatever and whenever they can, or risk starvation. Prey choice and/or active prey selectivity in these taxa must be discussed within this context.

Conceptual and/or numerical models that attempt to define feeding rate, prey choice or prey selectivity in small zooplanktivores always use AA as an input variable. Since VA is 3 orders of magnitude less than AA, this underscores the need to accurately characterise the perceptual abilities of the organisms in order to realistically parameterise such models. Failure to do so may result in interpretive and predictive errors about predator–prey dynamics in marine food webs.

How the northern krill perceives its prey: The northern krill *Meganyctiphanes norvegica*—an omnivorous predator—is an important component of the food web in North Atlantic ecosystems. Based upon (1) gut content analyses of field-caught animals; (2) net tows and hydroacoustic surveys in which the spatio-temporal overlap of krill and their potential prey are mapped; and (3) laboratory experiments of krill feeding rates in the light vs. the dark, it has been suggested that *M. norvegica* is a selective visual predator (Torgersen 2001, Kaartvedt et al. 2002). Although such observations can surely serve as an initial baseline, they tell us nothing about underlying mechanisms and

can therefore lead to misinterpretations. Recent work on *M. norvegica* (M.T. Breien & H.I. Browman unpubl.) provides a good example of how making such conclusions about the sensory basis of prey detection—without the benefit of empirical observations of sensory biology, sensor morphology, and behaviour—can lead us astray.

The responses of *Meganyctiphanes norvegica* to free-swimming copepods (*Calanus* spp.) were observed using silhouette video photography, which allowed quantification of predator–prey interactions (in 3-D, and at 25 frames s⁻¹). Attacks were characterised by a pronounced and directed movement of the krill's antennae, followed by a propulsion of the feeding basket towards the copepod. Prey detection distances differed slightly between experiments run in light vs dark (25 ± 9 and 22 ± 10 mm, respectively), but there were no differences in the position of the detected prey relative to the predator. Attacks were uniformly oriented laterally (in both light and dark), and in 80% of the cases detected prey were located below the krill's body axis, i.e. presumably outside its perceptual field. This indicates that mechanoreception, and not vision, is the main sensory modality involved in proximity prey detection by *M. norvegica*. Furthermore, the morphology of the *M. norvegica* eye (Hallberg & Nilsson 1983, Nilsson 1996, Dan-Eric Nilsson pers. comm.) is such that its spatial resolution is inadequate to detect small objects at close range. Rather, vision in this species is most likely important for detecting predators and clusters of prey (at a distance), and for other photobiological processes such as perceiving changes in light intensity. Breien & Browman (unpubl.) also observed avoidance behaviour in the copepods: escape responses carried them far beyond the krill's perceptual range. Since the perceptual field of *M. norvegica* is similar in volume to that of a small fish larva, there will only rarely be more than 1 prey item available to the predator at any given instant. Thus, the prey selectivity reported for this predator probably reflects its ability to catch a certain type of prey organism, rather than an active choice.

The preceding examples highlight how sensory biology is *required* to mechanistically link the organism's internal and external ecologies and, thereby, to make well-founded and accurate predictions about key processes in marine ecology.

Applications in aquaculture. Designing improved feeds for marine fish larvae: Intensive culture of marine fish larvae still depends upon live prey as the initial diet. Large-scale production of such prey is time-consuming and expensive. Thus, development of formulated microdiets (MD) that are readily consumed by larvae and juveniles is an essential step towards cost-effective farming of marine fishes.

Most of the research to develop MDs has focussed on nutritional quality, digestibility, size, and texture (e.g. Cahu & Zambonino Infante 2001, Koven et al. 2001). However, knowledge about how various constituents of the feed will affect feeding behaviour is also important to develop a successful commercial diet. Certain substances might attract larvae and motivate their feeding response. Such odours (and/or tastes) should be added to a formulated diet. Other substances might be repellent and suppress feeding. Such odours/tastes should be avoided. To be anthropomorphic: if the food that you place on your children's plate looks or smells 'wrong', they will not touch it, no matter how good it is for them. Why should fishes be any different?

Several studies have evaluated the sensitivity of fishes to various amino acids: the olfactory and gustatory systems of even very young fish respond to a wide variety of such substances (Yacoob et al. 2004 and references cited therein). Recent reports demonstrate that permeating formulated feeds with specific chemical odours can dramatically increase the growth rate of fish larvae (e.g. Kolkovski et al. 2000). Thus, identifying substances that can motivate the feeding response of marine fish larvae and increase the probability that they will retain and digest it, holds promise for the rapid improvement of formulated feeds.

Unfortunately, very little is known about the olfactory and gustatory responses of marine fish larvae. Electrophysiological and behavioural techniques can be used to generate concentration response curves for various substances and to characterize how the fish behaves in their presence. Essentially, these techniques permit us to ask these animals what smells and tastes they prefer: a very practical application of sensory biology.

Host-finding in the parasitic salmon louse: The salmon louse *Lepeophtheirus salmonis* is an ectoparasitic copepod that infests both wild and farmed salmonid fishes. Salmon lice are a major disease problem in farming of Atlantic salmon *Salmo salar* L., and the possibility of their playing a role in the decline of wild anadromous stocks has also been raised. Efforts to control this parasite in salmon farms have been limited to the use of chemical delousing agents and co-culture with cleaner fish (several species of wrasse). In recent years, the search for effective and long-term solutions to the problems caused by salmon lice—and other parasites of fishes—has turned from delousing treatments to improving our knowledge of louse biology. One aspect of this body of work focuses on the host-associated sensory stimuli that parasites might use to locate and discriminate a compatible host (e.g. Novales Flamarique et al. 2000, Mikheev et al. 2003, 2004, Browman et al. 2004).

Lepeophtheirus salmonis hatch as nauplius I larvae from egg strings carried by adult females attached to the host, and immediately commence a free-swimming planktonic lifestyle. The species' life cycle consists of several larval stages, culminating in male and female host-resident adults. The free-living larval forms must locate and attach to a suitable host in order to complete their life cycle. Characterizing the responses of the salmon louse to various host-related cues may eventually allow us to disrupt host location and settlement by inducing the parasite's free-living stages into swimming away from salmon sea cages or migratory routes (H.I. Browman et al. unpubl.; see Cardé & Minks 1995 for an example of related work on insects).

The sensory modalities and behaviour involved in host detection and recognition by the salmon louse appear to consist of a spatio-temporal hierarchy, within which 1 or more senses operate simultaneously. Visual cues—such as decreases in light intensity resulting from shadows cast down into the water column by fish swimming overhead—operate at a range of meters to 10s of meters. Such signals alter the parasite's overall activity level and/or swimming pattern, typically motivating it to move toward the source of the cue (Novales Flamarique et al. 2000, Mikheev et al. 2003). The salmon louse is, in fact, very sensitive to decreases in light intensity (Novales Flamarique et al. 2000). Increases in light intensity, such as flashes off the side of a fish, can also induce directed swimming behaviour, as is the case for the fish ectoparasite *Argulus foliaceus* (e.g. Mikheev et al. 2003). Light flashes would probably be visible over shorter distances than shadows. Diffuse chemical cues, such as the 'smell' of a large group of salmon on a migratory run or in sea cages, may also act as directional cues over scales of meters to 10s of meters, and they persist longer than a shadow or a light flash. A diffuse, host-related chemical cue could also alter the louse's response to visual cues, as is the case for the fish ectoparasite *Argulus coregoni*, which locates hosts more effectively using vision when olfactory cues are present (Mikheev et al. 2004). Thus, shadows, light flashes, and diffuse chemical cues can all attract a population of free-swimming lice towards a population of potential host fish over fairly long spatial scales. However, the chemical trails associated with a single fish operate on small spatio-temporal scales—perhaps only a few cm (e.g. Okubo et al. 2001, Ingvarsdóttir et al. 2002). For most copepods, hydrodynamic cues are also only effective on scales of mm to a maximum of 3 to 4 cm, and they are fleeting (e.g. Yen & Okubo 2002). This also appears to be true for salmon lice copepodids, which respond to a moving plaster cast of a salmon head over maximal distances of 3 to 4 cm (Heuch & Karlsen 1997, P. A.

Heuch unpubl. data and pers. comm.). Finally, at settlement, chemical and tactile cues associated with the surface of the host are probably most important (e.g. Buchmann & Bresciani 1998). Thus, over smaller spatio-temporal scales where vision is unimportant to the salmon louse, the parasite probably relies on olfactory and mechano-sensory cues to locate salmon (Browman et al. 2004).

Lighting in intensive culture systems: Even small changes in light intensity and 'quality' (i.e. spectral characteristics) can have significant effects on the feeding rate, survivorship and growth of marine organisms (e.g. Puvanendran & Brown 2002). Despite this, the choice of light environment in indoor intensive culture systems has, with few exceptions, been little more than guesswork. For example, fluorescent tubes are commonly used as light sources in such culture systems. The spectral emission of these tubes is narrow-band and centered on wavelengths that result in them looking white to *humans*. To marine organisms—whose visual systems are mostly sensitive at wavelengths different from those of humans—these lights will not look white at all, and they will not appear as intense to them as they do to us. In addition, unless we know the details of their spectral sensitivity, we are unable to evaluate *a priori* how easy (or difficult!) such lighting conditions might make it for them to detect food. Sensory biology can be used to characterize the spectral sensitivity of marine organisms and this knowledge can be applied—using colour theory (see Wyszecki & Stiles 2000)—to tailor the lighting conditions under which they are raised, e.g. to maximize the contrast of prey against the background of the tank.

Anthropogenic noise in intensive culture environments: There is currently very little information about the effects of acoustic stress on fish. Rearing conditions in aquaculture tanks can produce sound levels that are 20 to 50 dB higher than in natural aquatic habitats (Bart et al. 2001). Although attempts are often made to determine the most effective culture temperature, food quality, photoperiod, and water chemistry (among other environmental variables), little or no effort has been directed to determining the appropriate acoustic environment for optimal growth and development in marine fishes. The few studies that *have* examined the effects of sound on fishes in a culture context demonstrate that high levels of ambient sound can be detrimental to eggs and decrease larval growth rates (Banner & Hyatt 1973, Lagardère 1982). Elevated noise can damage the fish ear and stress the animals (Popper et al. 2004, Smith et al. 2004), and these effects may result in poorer growth rate and survival. To assess this, we must examine how the morphology of the ear is affected by noise, and make audiograms to characterize the organisms' ability to hear.

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 Chandross 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