

THEME SECTION

Sensory biology: linking the internal and external ecologies of marine organisms

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CONTENTS*

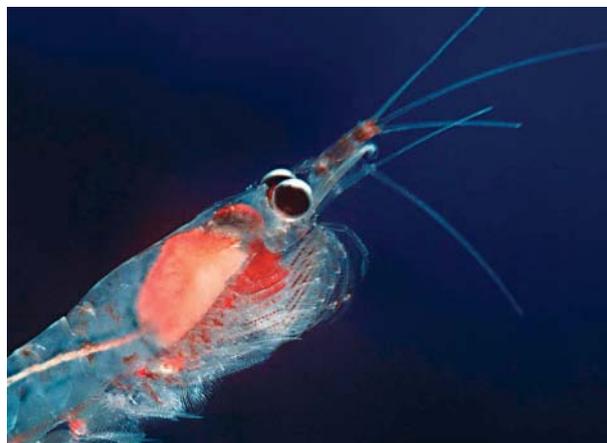
Weissburg MJ	
Introduction	263–265
Browman HI	
Applications of sensory biology in marine ecology and aquaculture	266–269
Fields DM, Weissburg MJ	
Evolutionary and ecological significance of mechanosensor morphology: copepods as a model system	269–274
Hemmi JM, Zeil J	
Animals as prey: perceptual limitations and behavioural options	274–278
Higgs DM	
Auditory cues as ecological signals for marine fishes	278–281
Johnsen S	
Visual ecology on the high seas	281–285
Mead KS	
Reception before perception: how fluid flow affects odor signal encounter by olfactory sensors	285–289
Mogdans J	
Adaptations of the fish lateral line for the analysis of hydrodynamic stimuli	289–292
Nevitt GA, Bonadonna F	
Seeing the world through the nose of a bird: new developments in the sensory ecology of procelariiform seabirds	292–295
Walker MM, Dennis TE	
Role of the magnetic sense in the distribution and abundance of marine animals	295–300
<i>Literature Cited</i>	300–307

Introduction

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Contributions to this Theme Section (TS) articulate an increasingly powerful synthesis in ecology: understanding animal perceptual abilities lends insight into ecological interactions that, in turn, determine fundamental properties of populations of organisms and communities. This synthesis, often referred to as sensory ecology (e.g. Dusenbery 1992), has its antecedents in diverse fields ranging from sensory physio-



Meganyctiphanes norvegica. Knowing which sensory modes the Northern krill uses to locate prey is central to evaluations of its feeding ecology. This Theme Section presents case studies that demonstrate 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. *Photo copyright Uwe Kils, Rutgers University. Used by permission*

logy, behavior and behavioral ecology, to classical population ecology (e.g. Lythgoe 1979, Dusenbery 1992, Endler 2000). However, it is unique in the explicit recognition that the capacity of organisms to acquire information from the environment is an essential determinant of ecological function. Thus, sensory ecology acts as the disciplinary interface between the processes occurring within organisms and those occurring between organisms and their environment.

The sub-discipline of sensory ecology is a relatively new endeavour. Although sensory physiology, behavior and ecology are all well established areas that have made substantial contributions to our understanding of the natural world, there is a distinct lack of studies that link the inner and outer ecologies of animals. The explanation for this may lie in a historical tendency to pursue specialized knowledge within a given level of inquiry at the expense of synthesis across levels (see Saarinen 1980). Whereas sensory physiologists largely address the mechanisms operating within organisms

*Contributions are in alphabetical order (by first author)

(or their cells), ecologists have often treated animals as black boxes whose inner workings are mysterious, irrelevant or assumed. Of course, it is not always necessary to understand how animals do things in order to advance the science of ecology. The importance of predation as a force structuring natural communities is plain even in the absence of detailed knowledge of how animals find their prey. Equally clear, however, is that information on perceptual mechanisms is sometimes indispensable for arriving at valid conclusions. For example, optimal foraging theory has been a useful heuristic tool, but has been less successful in predicting ecological outcomes, in part, because assumptions of perceptual capabilities (e.g. instantaneous recognition of prey types and their energetic value) are often unrealistic (Krebs & Davies 1991).

As documented in the contributions to this TS, a firm appreciation of sensory biology can provide insights into animal distributions, relationships among competitors, patterns of predation, and even life history or social structure. Further, understanding the role of animal perceptual abilities in determining ecological interactions has become more critical as evidence accumulates that flexible rules govern the responses of animals to the environment. In particular, a bevy of recent studies indicate that behavior, morphology and physiology may become altered in response to specific cues, in order to increase individual fitness in given environments. The changes—induced by competitors, predators or allies, and termed trait-mediated effects—often cascade through other community members to have dramatic consequences on community structure and function. These (indirect) trait-mediated effects can have as much impact on population and community properties as do 'direct' effects associated with alterations in the density of organisms engaged in competitive, predatory, or mutualistic interactions (Werner & Peacor 2003). For instance, aquatic herbivores alter their habitat use when they detect cues released by predators, and this behavioural shift has substantial effects on the algal and macrophyte community (Turner et al. 2000, Trussel et al. 2002). Understanding the conditions under which organisms can acquire sufficient information to implement plastic responses is necessary to predict where and when indirect effects occur.

This TS is designed to promote sensory ecology by documenting the specific, concrete and special ways in which it contributes to our understanding of marine ecology. The coverage of modalities, animal types and behaviours was designed to highlight the diverse areas in which understanding perceptual abilities provides ecological insight, but it will be left to the reader to come to conclusions regarding comparisons across sensory modes or taxa. This TS will permit a synthesis, but it is our belief that analyzing the ecological impact

of perception is in a very early phase. Thus, we need to cast the net broadly by encouraging comparative analyses rather than canalizing the discussion into particular lines. In this spirit, we have encouraged the contributors to discuss 'what may be', as opposed to simply summarizing 'what is', and to challenge the scientific community to help in ultimately discovering which of these speculations are true.

In spite of their large topical range, the contributions to this TS are united by several common themes. There is a robust focus on how the physical world affects signal properties and their transmission, since this initial process constrains an animal's ability to extract information from the environment. Although we appreciate that physical factors may be so harsh as to prevent mobile consumers from exploiting prey (e.g. Menge & Sutherland 1976), effects on sensory perception are more subtle and have not been well evaluated. These effects are potentially important, but may remain hidden without studies that examine search success, efficiency, or perceptive ranges in specific sensory environments. This TS provides numerous illustrations of how the physical environment limits the times and places in which animals can perform certain tasks, and of how particular environments may alter signals in ways that restrict the ability of animals to obtain information about potential predators, prey or mates. Determining how and why some environments produce poor sensory performance yields important and testable predictions about the relationship between population demographics and sensory mechanisms. The contributions to this TS by Browman, Fields & Weissburg, Johnsen, and Mead provide excellent examples of this line of reasoning, and show how the determination of an animal's sensory niche may provide insights regarding distributions of related or competing species. Similarly, the contributions by Higgs, Nevitt & Bonadonna, and Walker & Dennis discuss how the mere existence of particular sensory modes may have close associations with population structure and distributions. One inescapable conclusion from these essays is that we know remarkably little about natural signals. Vision is perhaps the most accessible and intuitive sensory mode for a human investigator. Yet Browman, Hemmi & Zeil, and Johnsen (in this TS) point out how we are sometimes blinded by applying our idiosyncratic visual perspective to other animals. Our appreciation of other sensory signals, particularly chemical and fluid mechanical cues, is even more rudimentary, because human perception provides no useful guide and because we have only recently been able to examine the structure of these signals over biologically relevant temporal and spatial scales.

A second thread running through the contributions in this TS is the interrelationship of form and function.

Our understanding of sensory processes is sometimes sufficient to establish how and why particular sensory mechanisms are adaptive in given environments or for particular tasks. This classical adaptive or evolutionary reasoning is turned on its head when several contributors ask whether ecological function may be related to sensory abilities. This does not reflect a particular view of how behavioural or sensory systems evolve. Rather, trying to infer function from form is an inquiry into whether understanding perceptual mechanisms permits robust ecological predictions. Thus, in this TS, Fields & Weissburg, Hemmi & Zeil, Mead, and Mogdans incorporate knowledge of how sensory systems may be tuned to detect particular signal sources, to generate hypotheses regarding patterns of prey selectivity or predator avoidance. Using morphological, anatomical and physiological aspects of sensory systems to determine favoured prey, or feared predators, may enable predictions on ecological relationships between organisms for which direct behavioural observations are difficult or impossible. These contributions discuss both the potential and the difficulties inherent in this type of analysis.

Several authors make the critical, but perhaps unappreciated point that sensory systems are embedded in a complex substrate—the organism. Several ecologically relevant lessons emerge from this observation: (1) It appears that sensory mechanisms may influence, or may be related to, a variety of organismal traits not generally associated with perception: the contribution by Walker & Dennis provides a particularly compelling example of how the usage of particular magnetic signal properties may be contingent on social systems and life-history; Nevitt & Bonadonna examine the possibility that certain olfactory foraging strategies may be favoured because of particular lifestyles, and that perceptual mode is associated with an ensemble of characteristics that uniquely characterizes a particular ecological niche. (2) The ecological significance of sensory abilities may change with life history stage, and thus, the stage at which an organism possesses a particular attribute may be as important as whether it possesses it at all; the contribution by Higgs supplies a relevant example by discussing the role of hearing in fish larvae; his analysis suggests that small changes in ontogenetic trajectories that result in an earlier expression of particular traits, as opposed to final properties of the auditory system, may have a large influence on how hearing affects ecological properties. (3) Learning, memory and other long term changes in neural substrates that interact with sensory systems may have an impact on what information an animal extracts from the environment. We tend to analyze sensory properties as if they were static, but take this

approach at our peril; animals frequently use a hierarchy of cues to establish risk, and these cues may change over time, as animals learn to ignore irrelevant stimuli. Thus, determining how sensory systems resolve risk level and how risk perception may change over time will increase our understanding of threat avoidance behaviour. Hemmi & Zeil point out how behavioural ecology may derive considerable benefit from examining temporal changes in the utilization of sensory information underlying risk perception.

Finally, ecology is frequently an applied endeavour as we seek to conserve and manage wild and captive animal populations. Thus, many of the contributors to this TS have emphasized that understanding sensory mechanisms is a useful starting point in a variety of practical ecological applications. Higgs and Johnsen, for example, discuss how analyzing perceptual mechanisms may improve our ability to predict the ecological impact of anthropogenic changes. Browman gives several examples of how understanding sensation can increase the economic efficiency of mariculture and reduce the negative side effects that degrade environmental quality. These contributions emphasize how knowledge of sensory mechanisms is an important, but often neglected, tool that improves our ability to cope with current challenges to ecosystem health and resource management.

One of our goals for this TS is to promote an appreciation for sensory ecology, and encourage investigators to incorporate a more explicit sensory component in their own work. Thus, we have used this TS to illustrate the wide range of questions, approaches and levels where knowledge of perceptual mechanisms can provide insight into ecological issues. The essays themselves will perhaps serve to both inspire readers, and they may also form a template for future work. Sensory ecology occupies the interface between the inner and outer worlds of animals, but also exists at the transition between abiotic and biotic factors; perceptual systems represent a transfer function, transforming physical stimuli into ecological effects via behavioural acts of the animal. As ecologists concerned with the relationships of animals to their biotic and abiotic environment, much of what we study has an implicit, if not explicit, relationship to this transfer function, even when we treat the animal as a black box. We hope that you will be inspired to take the lid off, peek inside, and be amazed!

Acknowledgements. This theme session is dedicated to Dr. David Dusenbery. Dr. Dusenbery's insights into how the physical world constrains the biology and ecology of information gathering forms one of the cornerstones of sensory ecology. As both friend and colleague, he has made immeasurable contributions to our own work, as well as the work of others.

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: Gallagher 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 (Yacoub 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 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; Alcazar & 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

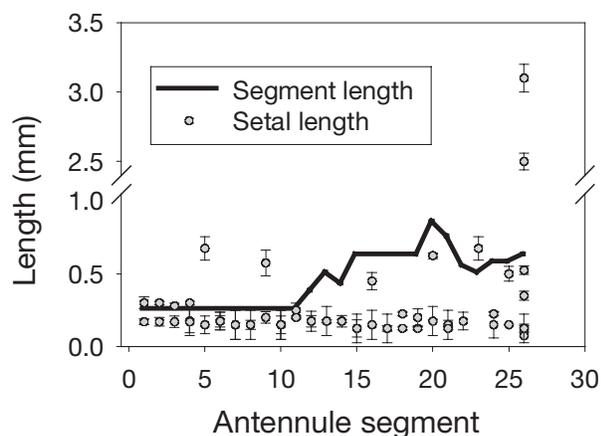


Fig. 1. *Gaussia princeps*. Antennule morphology. Dots represent setal length of individual hairs (\pm SE, $n = 6$). Solid line shows segment length. Note the increase in length at segment 11

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

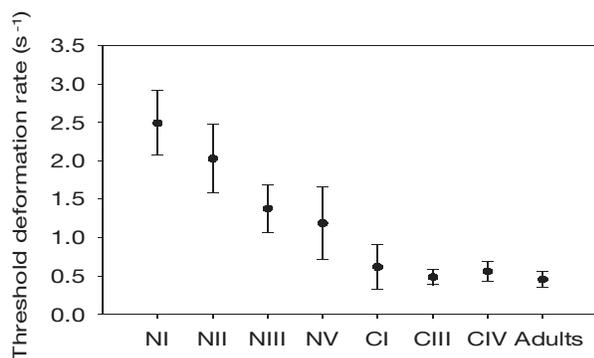


Fig. 2. *Acartia tonsa*. Escape threshold ($\pm 95\%$ CI) of developmental stages from a siphon flow (Redrawn from Kjørboe et al. 1999)

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

and behavioural options of animals faced with predation pressure. We argue this point from the perspective of a fiddler crab *Uca vomeris*. Fiddler crabs are a common prey animal in estuarine ecosystems and an important food source for a number of seabirds, which catch them using a variety of hunting techniques (e.g. Iribarne & Martinez 1999). The crabs represent a 'bonsai' version of a predator-affected animal society; fiddler crabs constitute a dense population of burrow-centred, small home-range foragers that allow us to investigate the relationship between the predictive quality of sensory information and the organization of predator avoidance behaviour in unprecedented detail. Their entire behavioural repertoire, including their distinct, well-defined predator evasion responses can be monitored continuously over extended periods of time. The crabs respond to predators using exclusively visual cues and the relevant properties of their eyes are known (Land & Layne 1995, Zeil & Al-Mutairi 1996). Crabs make no directed or scanning eye movements because they possess a panoramic visual field. Consequently, we can quantify precisely what a crab sees while recording what it does (e.g. Hemmi & Zeil 2003, Hemmi 2005a,b). Furthermore, the visual information available to the crabs throughout a predation event can be manipulated precisely (Hemmi & Zeil 2003, Hemmi 2005a,b). For instance, by simulating the 'trawling' flights of one of the crabs' main predators, the gull-billed tern *Sterna nilotica* (Land 1999), with dummies, we can measure the quality of sensory information as the correlation strength between visual cues (the dummy's apparent size, speed and position on the eye) and the dummy's real size, speed, distance and direction of approach. We can thus estimate the actual predation risk as a function of the distance and the direction of a dummy's approach.

Perceptual constraints and risk assessment. Crabs see predators before predators see crabs in most cases, because the predators are larger than the crabs themselves. This large size difference compensates for the extremely poor resolving power of crab eyes relative to a typical bird predator (Land & Layne 1995, Zeil & Al-Mutairi 1996). However, detecting a predator does not mean knowing the risk it poses. At least initially, there is no robust correlation between sensory (visual) cues available to a prey and the actual movements of a predator. We consider this information deficit to be the key to understanding why evasive actions of prey animals are so similar across species: many species respond to real and dummy predators in 6 distinct stages, each indicating a different level of perceived threat and each characterized by specific cues, consequences and costs (Table 1). We suggest that predator evasion is an optimising task, in which prey animals attempt to increase the quality of information, in order to delay or avoid costly responses without taking significant risks.

Our working hypothesis is that the multi-stage predator avoidance behaviour reflects the prey's initial deficit of accurate information on a predator's distance, speed and direction of approach. As the response progresses and costs escalate through 'freeze', 'home run' and 'burrow entry', animals become more selective in what they respond to, because they gain increasingly accurate information on a predator's distance and approach direction. For instance, crabs run home when the bird or dummy they have detected is still so far away and small that they have no information on its shape, its distance or its approach direction (Hemmi 2005b). Crabs cannot determine the real distance of a predator with their closely set, low-resolution eyes, but instead rely on indirect cues like angular size, the change of which is correlated with change in distance.

Table 1. *Uca vomeris*. Stages of predator avoidance behaviour in fiddler crabs

Activity	Description	Function/consequences	Cost	Visual cues
Freeze	Stop activity, remain motionless	Gathering information, reducing conspicuousness	Low	Detection threshold ^a
Home run	Return to burrow entrance	Reducing risk	Energy, conspicuousness	Apparent speed looming? ^b
Burrow vigilance	Stay at burrow entrance	Gathering information, reducing conspicuousness	Lost opportunities	?
Burrow entry	Escape underground	Reducing risk	Loss of information	Looming ?
Burrow time	Stay in burrow	Avoiding risk	Lost opportunities	N/A
Re-surfacing vigilance	Stay at entrance before resuming normal activity	Gathering information	Lost opportunities	?

^aCrabs appear to freeze in response to any distant object moving above the horizon
^bHome runs can be triggered by objects when they are just detectable by the crabs' eyes or by a just detectable apparent movement

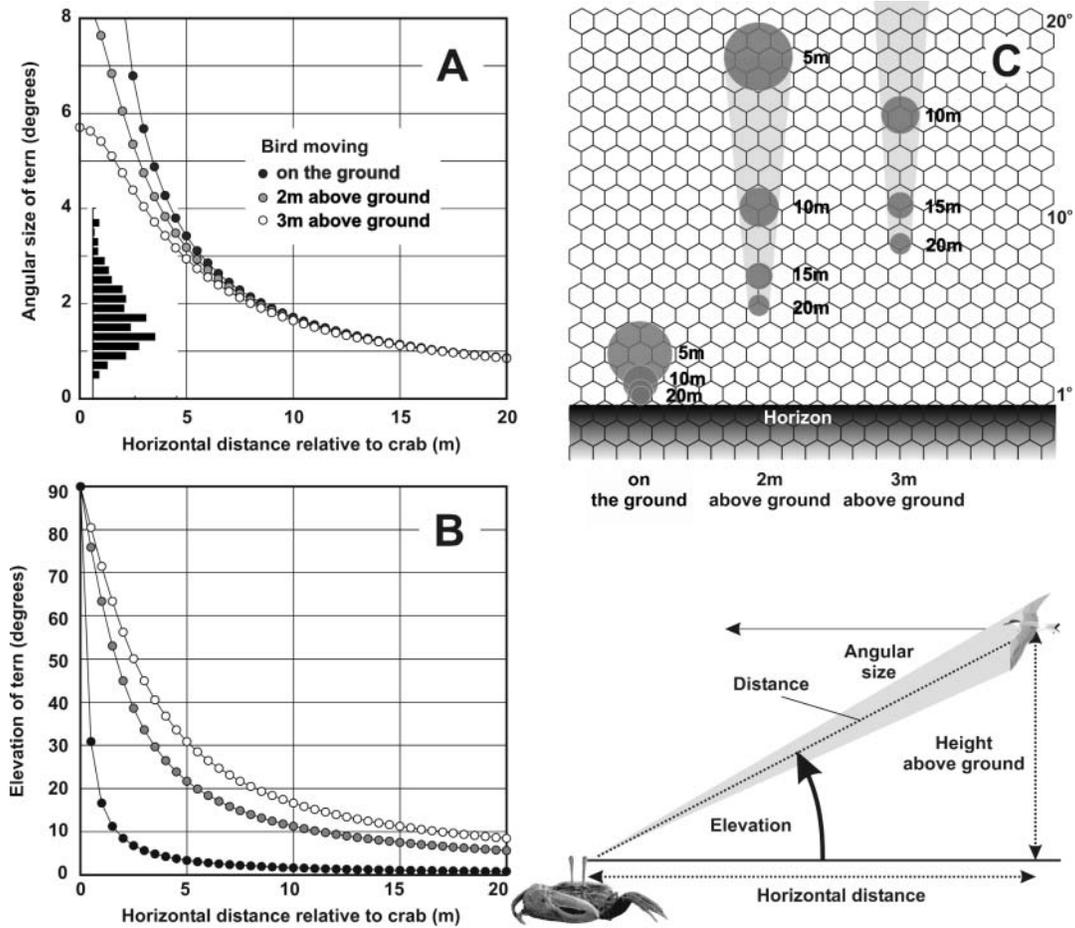


Fig. 3. *Uca vomeris*. Visual geometry of predation in fiddler crabs. (A) How the angular size of a 30 cm large bird changes with horizontal distance, when it is approaching on the ground, or flying 2 m or 3 m above the ground (see schematic drawing on bottom right). The inset shows the frequency distribution of the angular sizes of dummy predators at the moment crabs initiate their home runs (from Hemmi 2005b). (B) How the elevation of the bird's image in the visual field of a crab changes with horizontal distance. Conventions as in A. (C) Angular positions and sizes of the walking bird and the bird flying at 2 m and 3 m projected onto the facet array of a fiddler crab eye for horizontal distances of 20 m, 15 m, 10 m and 5 m (see also Land & Layne 1995). Inter-facet angle is assumed to be uniformly 1° , which ignores the fact that the resolving power of the fiddler crab eyes varies significantly across the visual field (Land & Layne 1995, Zeil & Al-Mutairi 1996)

We stress that many small prey animals likely face such a deficit in accurate information. For example, lizards visual cues to distance, like binocular stereopsis, are restricted to close range and to the frontal visual field (see Collett & Harkness 1982). We illustrate this visual geometry of predation in Fig. 3 from the viewpoint of a crab by considering 3 simple cases of a 30 cm bird approaching on the ground, or flying at 2 m and 3 m parallel to the ground. The figure shows how the apparent size (Fig. 3A) and the elevation of the bird (Fig. 3B) increases as it approaches, together with the frequency distribution of apparent sizes at the moment crabs respond to dummy predators (inset histogram in Fig. 3A). Note that 'home runs' are triggered when the bird is between 5 and 20 m away, even though it is seen by a maximum of 3 receptors (ommatidia), which sample the world with a resolution of about 1° (Fig. 3C).

Interestingly, the crabs respond earlier when a dummy bird flies past them compared to when it approaches them directly (Land & Layne 1995, Hemmi 2005a). Despite the fact that the directly approaching predator poses a higher risk, the crabs allow it to come closer! The reason for this counterintuitive result is that crabs use the apparent speed of the predator to trigger their 'home runs' because more reliable indicators of predation risk are not available at this stage. The apparent speed of a directly approaching object is much lower than the speed of an object that will pass at some distance. The image of the 'bird' flying 2 m above ground (Fig. 3), traverses more than 3 receptors or ommatidial rows as it approaches from 15 m to 10 m, while at the same distances a bird approaching directly on the ground just begins to be seen by a second row of receptors. This lack of accurate information means that

the initial visual cues the crabs can detect about a predator do not allow them to predict actual risk. Because of this ambiguity, a harmless event like a passing bird is treated as more dangerous than a truly precarious situation posed by a directly attacking bird (Hemmi 2005a). This example teaches us an important general lesson: the behaviour of prey is not only influenced by the actual risk of predation, which can be measured as the probability of a prey animal succumbing to an attack, but also by the subjective or perceived risk, which needs to be measured from the prey's perspective, through the constraints of its sensory systems. The long-term indirect consequences of predation pressure on prey behaviour are, therefore, not determined by the actual risk, but by the prey's assessment of risk.

Coping with a hypersensitive early warning system.

The initial lack of accurate information on predation risk forces prey animals to adopt an early warning system that is very sensitive, reliable and safe, but that is consequently unspecific. Prey animals like fiddler crabs therefore face a second problem: if early predator detection is by necessity unselective, how do they avoid responding to everything that moves in their environment, be it dangerous or not? For fiddler crabs, the answer is that they do indeed respond to almost everything that moves in the sky (Layne 1998). However, they use at least 2 strategies to reduce the cost of false responses:

(1) The crabs organize escape into distinct stages (Table 1), and this allows them to be highly selective in initiating the final and probably most costly stage of their escape, 'burrow entry'. The crabs' 'home run', triggered by apparent movement, usually stops at the burrow entrance. The functional significance of this behaviour can be understood by considering the main cost associated with entering the burrow: the total loss of information about a predator's position and movement. The moment crabs go underground, they enter a risky and time consuming 'waiting game' with their predator (Jennions et al. 2003, Hugie 2004). Once the crabs have reached the safety of their burrow entrance, they can afford to let the predator approach more closely, which gives them access to reliable indicators of approach direction (and therefore risk) such as looming cues (Nalbach 1990). This phase of 'burrow vigilance' improves risk assessment and thereby helps to minimize the escalation of costs (Koga et al. 2001). 'Burrow vigilance' also provides crabs with more accurate information on the type of predator they are facing. If the crabs have to play a waiting game with their attacker, the duration of this game should depend on the hunting technique of the predator. A tern that makes large-scale trawling sweeps across the mudflat (e.g. Land 1999) should require a much shorter waiting time than a plover running after, and waiting for, individual crabs (e.g. Zwarts 1985, Hugie 2004). The

improved ability of prey animals to assess the actual risk of predation once they are close to their refuge plays an important role in limiting the indirect effects predators have on their prey.

(2) The crabs avoid false responses by learning to ignore irrelevant objects and events (Walker 1972). Response strength declines when confronted with successive events of the same kind, a process called habituation (Peeke & Petrinovich 1984). Habituation has to be highly specific to help crabs minimize false alarms. For instance, despite the fact that 'home runs' are triggered by very sensitive and non-selective cues (Hemmi 2005b), crabs quickly learn to ignore a human observer or a mangrove tree moving in the wind. 'Home runs' do not habituate when the crabs are confronted with horizontally approaching bird dummies even after 50 presentations (Hemmi 2005a), but habituate rapidly when crabs experience a variety of other stimuli (Hemmi & Zeil 2001). We know little about the rules of habituation, but in the context of predator evasion, an interesting possibility is that animals employ habituation to improve response selectivity in the early stages of their behavioural sequence (e.g. 'home run') by using the information that they have previously gained from the relative safety of subsequent response stages (e.g. 'burrow vigilance'). The underlying rules of habituation will determine the kinds of non-predator related movements the animals can cope with, without constantly being alarmed. This will therefore have important consequences on the type of ecological settings the animal can live in. For instance, the rules of habituation in crabs allow them to fully ignore the motion produced by moving branches of a nearby tree, even though such motion would normally trigger an escape response.

In addition to these short-term behavioural strategies, fiddler crabs also show surprisingly flexible, long-term behavioural changes in response to predation pressure. They are able to choose, depending upon the perceived risk of predation, whether to go on long foraging excursions or not (Ens et al. 1993), they can modify their social signals, such as body colouration (Zeil & Hofmann 2001), and switch from one mating strategy, in which females have to take the risk of 'wandering', to another, where males have to leave their burrows to find receptive females (Koga et al. 1998). The information processing on which prey animals base the 'risk assessment' that underlies such long-term changes of behaviour is poorly understood, but again has important consequences on how animals respond to different environmental settings. Understanding the sensory information that underlies such long-term behavioural changes could, for instance, allow us to predict exactly under which conditions we expect to find one or the other mating system (Koga et al. 1998).

Predator strategies. Fiddler crabs are difficult to catch (Backwell et al. 1998), because they employ a multi-stage predator evasion response, because they are fast (up to 70 cm s^{-1} ; Layne et al. 2003, Hemmi 2005a), and because they are extremely good at locating their invisible burrow, an ability based on path integration (Zeil 1998). Not surprisingly, predators are forced to develop a variety of hunting strategies to catch crabs. One example of a predator that is able to catch resident crabs at their burrow entrance is the fast running great-tailed grackle *Quiscalus mexicanus* (Koga et al. 2001). These birds employ a trick to improve their success: they first run past the crabs and then turn back sharply to catch them, apparently disarming the mechanism with which fiddler crabs decide when to enter their burrow. Flying birds, on the other hand, like the terns at our study site in Townsville, Australia, never attempt to catch resident crabs by a direct approach. Instead, they have developed a trawling strategy, which empties the mudflat in front of them of resident crabs that scuttle into their burrows, but leaves wanderers and possibly surface-mating pairs exposed. The predictable and relatively brief hiding time of some fiddler crab species (e.g. Jennions et al. 2003) would suggest another rewarding strategy. Iribarne & Martinez (1999) found that black-bellied plovers *Pluvialis squatarola* often stand still near burrow entrances and wait until a crab emerges. Interestingly, however, these birds not only sit and wait, but use a mixed strategy: they spend a short time in a given location, either waiting for the few, unusually early crabs, or for those that had been underground at the time the bird approached. While waiting, the birds survey more distant crabs which are active on the surface and decide to chase them if the sit and wait strategy fails to deliver a re-surfacing crab (Iribarne & Martinez 1999).

Summary and outlook. Predation affects virtually every aspect of animal ecology. Our case study of fiddler crabs illustrates that prey animals employ different levels of behavioural flexibility to cope with information uncertainty and with the predation risk they face when foraging and searching for a mate. Lifestyle, behaviour, navigational skills, sensory abilities, behavioural options, and environmental topography all aid, and limit, the ability of prey animals to detect and evaluate the danger posed by their predators. The mechanisms of sensory information processing and their limitations have a significant influence on strategies of decision making under pressure and on the behavioural options prey animals have to balance risks and costs. We therefore argue that an 'ecology of information processing' is needed to fully understand the behavioural ecology, the evolution, and the dynamics of predator-prey relations.

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Auditory cues as ecological signals for marine fishes

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To become an ecologically relevant signal sound must: (1) be predictably produced in space or time, (2) travel some distance away from the immediate area of production, (3) be within the detectable frequency range of a species, (4) be above the hearing threshold of a species, and (5) carry information relevant to the animal. In other words, demonstrating that an animal can 'detect' an acoustic signal in a laboratory setting provides no information on the ecological role of the sound. Although there are few studies that examine all 5 of these criteria concurrently, there is enough information in separate studies to assess the potential role of sound as an ecologically relevant stimulus for fishes.

The role of sound as an ecologically relevant stimulus has been examined most extensively in the context of mate attraction and reproduction. Although many fishes produce sound during reproductive events (Ladich 2004), the ecological relevance of sounds can only be assessed by examining their behavioural effects on other individuals (the putative receivers). Responses of fish to conspecific vocalizations indicate that many fish species can use sound as a mechanism to detect and localize conspecifics (e.g. Tavolga 1956, Myrberg et al. 1986, McKibben & Bass 1998). The distance over which sound can be useful is often limited by the physics of sound travel underwater and therefore makes most reproductive sounds of limited use as an ecological cue over larger distances. Reproductive calls are often thought to be undetectable to fish within 20 m or less from the source, due to interactions with the surface and substrate (Mann & Lobel 1997), although the detection distance will increase as water depth increases. Theory predicts that territory size in soniferous species should reflect ambient noise conditions (Myrberg 1980), with fish inhabiting shallow, noisier, waters having smaller territories than related fishes in quiet, deeper waters. This idea has not been explicitly tested but would be a useful approach to discerning the ecological importance of sound in a reproductive context, especially in fishes that are known to produce stereotyped spawning sounds, such as midshipman *Porichthys notatus* (e.g. McKibben & Bass 1998).

Hearing in larvae of reef fishes. Many species of reef fish spawn floating eggs that are dispersed away from their spawning habitat. After hatching, larvae must find their way back to the reef in order to survive,

and it remains a mystery how fish larvae as small as 10 mm total length can accomplish this task. Although it is no longer assumed that larvae act as passive particles (see Montgomery et al. 2001), active mechanisms of recruitment are still being debated. Fish larvae exhibit behaviour that may enhance their ability to arrive at the reef either via directed horizontal swimming (e.g. Leis et al. 1996) or selective tidal stream transport (e.g. Forward et al. 1999). The larvae of many reef fishes show strong swimming abilities and some can potentially swim 50 to 70 km before exhaustion (e.g. Fisher et al. 2000), providing an active means of migration to the reef. If larvae are indeed actively locating and moving towards the reef, they must have some cue to find it. One such cue that has attracted recent study is the use of sound.

Reefs are particularly noisy environments, with biological sources raising sound levels to 30 to 50 decibels (dB) above non-biological background levels (e.g. Cato 1978). Much of the sound signature emitted from reefs is actively produced by adult fishes and invertebrates, resulting in an underwater 'chorus' that is produced in predictable time patterns for periods of several weeks (Cato 1978, McCauley & Cato 2000). These choruses remain up to 20 dB above background noise levels at distances of 5 to 8 km from the reef (McCauley & Cato 2000) and thus could provide a reliable cue for larval navigation. The predominant frequencies of these choruses are between 800 Hz and 1.6 kHz (Cato 1978), well within the detectable frequency bandwidth of adults and larvae of many species of reef fish (e.g. Myrberg 1980, Fay 1988, Kenyon 1996). Other species of reef fishes (hearing 'generalists', e.g. Blenniidae, Gobiidae) do not detect sounds above about 500 Hz and, therefore, would not be expected to hear the predominant reef frequencies, even close to the source. A comparative study of directed swimming in hearing specialists (those that can detect sounds above 500 Hz) and hearing generalists therefore may clarify the importance of sound as a cue for reef fish and may explain the mixed results often reported in studies using reef sounds as an attractant (e.g. Leis et al. 2003, see below).

These studies suggest that criteria (1) to (3) above are met for the larvae of at least some species of reef fish. Whether larvae are able to detect sound intensity and derive directional information from reef sounds is more difficult to assess. Although adult fish can obtain directional information from sound sources (Fay & Edds-Walton 2000), the precise time at which this ability first develops in larvae is not known.

Correlating ontogenetic changes in structure and function can be a robust technique for testing hypotheses related to an animal's sensory ecology (e.g. Blaxter & Fuiman 1990), and should be a fruitful avenue of

future research for directional hearing. Most marine fishes hatch with an undeveloped ear, and auditory structures become fully functional some time later (Fuiman et al. 2004). Fishes probably need hair cells of differing orientation to discern sound source direction (Fay & Edds-Walton 2000), but when hair cell orientation develops in marine species is not known. As fish larvae are at substantial risk of predation while in the pelagic environment, increases in the rate of auditory development may be a selective advantage if sound is an important cue. Examining auditory development in related species that are advected off the reef vs. those that remain in the reef environment might be a powerful test of the selective importance of sound in larval orientation.

The level at which a fish is said to detect sound depends upon the frequency of the sound, the technique used to measure responses (reviewed in Fay 1988), and may vary in the course of development (Kenyon 1996). Physiological thresholds for more sensitive species are often around 90 to 110 dB re 1 μ Pa (dB re 1 μ Pa is sound pressure emitted relative to a reference pressure of 1 μ Pa, a common decibel scale for underwater sounds) at peak frequencies (Fay 1988), but physiological methods often overestimate true thresholds by 30 dB or more (e.g. Brittan-Powell et al. 2002). Source levels of fish choruses on reefs attain up to 140 to 160 dB re 1 μ Pa at 1 m distance (McCauley & Cato 2000). A fish that has a behavioural threshold for hearing of 80 dB re 1 μ Pa would be able to detect reef choruses over 1 km away, assuming a typical spreading loss (rate of sound attenuation) of 6 dB/doubling of distance (Leis et al. 2003). The audible distance will be even greater for an entire reef (McCauley & Cato 2000). The degree of pelagic dispersion of fish eggs and larvae will differ between species (e.g. Ramírez-Mella & García-Sais 2003), but many species remain close enough to the reef to detect acoustic information. Thus, reefs do emit sound within the range of detectable frequencies and sensitivities expected for many adults found on reefs, although one has to be careful when extrapolating to reef fish larvae until more is known about the development of their hearing abilities.

Convincing tests of whether reef fish use sound as an important ecological cue for settlement must be conducted in the field using natural sounds. Only in this way can we determine whether fishes truly use the information they are capable of detecting. This approach has been applied in a small number of studies, with mixed results. Two studies used a combination of light traps with and without speakers broadcasting reef sounds to show that some species (Tripterygiidae: Tolimieri et al. 2000; Apogonidae, Mullidae, Pomacentridae: Leis et al. 2003) were preferentially attracted to

light traps with sound, whereas other species (Clupeidae: Tolimieri et al. 2000; e.g. Blenniidae, Chaetodontidae, Lutjanidae: Leis et al. 2003) showed no preference for noisy light traps. Although the authors of both studies suggest that these results show the importance of hearing as an attractant, that is not the only possible explanation. In both studies, it is possible that light was the main attractant and, as larvae approached the trap, vibrations from the speaker stimulated their neuromasts. Thus, mechanosensory, rather than auditory, information transmitted by the speaker may have selectively enhanced the catch in the 'noisy' trap. One way around this problem would be to set out traps with only sound cues. The catches of 'lightless' traps, with and without speakers, could then be compared. 'Noisy' traps should capture more reef larvae if sound really were the predominant cue for settling and if the larvae could localize the sound source.

An intriguing, but labour intensive, technique of following free-swimming larvae in open water has recently been used to examine the role of sound as an attractant. Leis et al. (2002) followed free-swimming *Chromis tripteronalis* (Pomacentridae) settlement-stage larvae in the presence of different sound treatments (no sound, broadcast reef sounds, and artificial noise). In the absence of broadcast reef sounds, *C. tripteronalis* larvae swam in a southerly direction, but when nocturnal reef sounds were broadcast, the average directionality broke down. These results led Leis et al. (2002) to suggest that larvae can use reef sounds as a cue for settlement (since they seemed to hear them and change behaviour) and that larvae can distinguish between relevant (reef) and irrelevant (anthropogenic) sounds. Interestingly, the larvae never swam toward the speaker broadcasting nocturnal reef sounds, they just changed direction. Part of the lack of attraction may have been a result of playing nocturnal reef sounds during the day. Further, fish probably use multiple cues to find the reef (Kingsford et al. 2002), so nocturnal sounds reaching the ear while light reaches the eye may disorient the animal. As it is clearly impossible to conduct free-field following experiments at night, when most larval settlement occurs, these studies may not be the most effective way to examine the use of sound for settlement, although they remain an interesting method for examining natural behaviour in reef larvae.

Finally, Tolimieri et al. (2002) used selection chambers to test behavioural preference of triplefin *Fosterygion* spp. (Tripterygiidae) larvae in response to reef sounds. Triplefin larvae moved toward the speaker that was broadcasting reef sound at night, but moved away from the reef speaker during the day. This suggests that these larvae can indeed use reef sounds as an attractant and can obtain directional information from them. However, more studies of this type must be

conducted, and with a greater diversity of species, before the role of sound as an attractant to reef larvae can be properly assessed. If sounds are an important determinant of larval recruitment, this may help explain why some species have dispersal of eggs or larvae, whereas other species retain eggs and larvae on the reef. Hearing specialists may be more likely to disperse progeny, whereas hearing generalists may retain progeny closer to the reef environment, an idea as yet untested but potentially fruitful.

Hearing in non-reef fishes. One interesting aspect that has been ignored thus far is the role that sound might play as an attractant in non-reef larvae. Many coastal marine fishes are broadcast spawners and emit mating sounds in large spawning aggregations. The eggs are then advected offshore and the larvae must find their way back inshore to survive, analogous to the situation for reef larvae. Whether larvae find their way back to estuarine waters by passive dispersal or active behavioural modification remains to be clarified. It would be very valuable to perform behavioural and physiological experiments in pelagic species that must return to estuarine waters, in comparison to species that stay in estuaries throughout life. A useful group in this regard might be the family Sciaenidae, which includes species that spawn offshore and move inshore as larvae (Atlantic croaker *Micropogonias undulatus*), species that develop entirely inshore (spotted seatrout *Cynoscion nebulosus*). If sound is an important attractant to pelagic fish larvae, then the Atlantic croaker should have more sensitive hearing to coastal sounds than seatrout. By using this comparative approach, we should be able to examine evolutionary questions (e.g. how many times did high frequency hearing evolve and in which environments?) as well as assess the prevalence of sound as an attractant.

The ecological role of sound has not been tested in enough detail, but auditory stimuli may be important in a variety of contexts. There is some evidence for a role of hearing in predator-prey relations of marine fishes, but this needs to be pursued. Sharks are attracted to pulsed sounds made by struggling fish, and by simulations of such sounds, with attraction occurring over many meters (Myrberg 2001). Other marine fishes might use sound to detect predators, but responses to predator sounds have not been explicitly studied. American shad *Alosa sapidissima* can detect (Mann et al. 2001) and show evasive maneuvers to (Plachta & Popper 2003) ultrasonic frequencies in the laboratory and the authors suggested that this high frequency hearing is a mechanism to detect and avoid echolocating dolphins. Cod *Gadus morhua* also detect ultrasonic tones, again perhaps as a mechanism to avoid dolphin predation (Astrup & Møhl 1993). Playback experiments are necessary to demonstrate con-

clusively that marine fishes use sound to detect prey or predators. The experiments would ideally consist of fish held in a container large enough to reduce distortion of sound fields, perhaps a net pen in open water with the speakers some distance away. Upon playing natural sounds through the speakers (either of predators or prey, depending on the experiment), movements of fish should be tracked to quantify whether they go towards (for prey sounds) or away from (for predator sounds) the active speaker. If active responses are seen, the behavioural threshold should be tracked to determine whether the levels at which fish respond are ecologically relevant. The same approach could be used to ascertain the ecological role of sounds associated with schooling (Denton & Gray 1993) and feeding (Amorim & Hawkins 2000).

Anthropogenic impacts. The effect of anthropogenic sounds in the marine environment assumes greater significance if fishes rely upon sound to obtain important ecological information. Shipping noise and sound bursts associated with oil exploration and military exercises can disrupt marine mammal populations, with potentially dramatic effects (Richardson et al. 1986), and there is a growing body of evidence for similar effects on fishes (e.g. Engås et al. 1996, McCauley et al. 2003). Further research is needed to explore the effects of anthropogenic sounds on fish populations, and more information about this environmental stressor is necessary immediately to support the choice of locations for marine reserves. Although reserves typically just restrict fishing activity, restrictions on anthropogenic noise sources close to the reserves are worth considering.

Conclusion. CAN fishes use sound as an ecological cue? The answer is yes. Reproductive sounds have been shown to attract fishes in the absence of other cues and there is growing evidence that fishes orient to sound signatures emitted from habitats, prey, and predators. DO fishes use sound as an important ecological cue in non-reproductive contexts? This remains to be proven. More studies, conducted under ecologically relevant conditions, are required to resolve these issues.

Visual ecology on the high seas

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Oceanographic research has focused on supra-organismal questions, particularly those involving abundance, distribution and trophic relationships. This approach has been extraordinarily productive and has

culminated in remote sensing techniques that can map the chlorophyll distribution in the surface waters of the entire planet on a daily basis. In contrast, our understanding of the physiology of the species eating this chlorophyll is in its infancy, particularly compared to what is known about coastal and terrestrial species. This is unfortunate, because understanding the physiology of pelagic species is essential for understanding their distributions, abundance, energy budgets and overall ecology. For example, the respiratory physiology of crustaceans and fishes affect their ability to colonize the oxygen minimum layer (Childress & Seibel 1998), and the different strategies for buoyancy in molluscs have significant effects on energy expenditure.

Recently, however, interest in the relationship between the physiology and ecology of pelagic species has increased. A large fraction of this work has centered on sensory physiology, a subfield of which attempts to relate the visual capabilities and optical properties of pelagic species to their behavior, distribution, and diversity. Dramatic improvements in the portability, reliability and cost of optical and neurophysiological equipment, combined with better computational tools, have led to increased research in this field. This article discusses 3 recent advances in the visual ecology of oceanic organisms and identifies several important, but as yet poorly understood issues. A common theme is the highly variable nature of the underwater visual environment, compared to most terrestrial environments. Illumination and turbidity levels can change dramatically due to both natural and anthropogenic factors, and this has important consequences for predation, mating and other activities. How these changes interact with other physical and biological variables to influence pelagic ecology will continue to be a fruitful area of research.

Recent advances in pelagic visual ecology. Vision in the ultraviolet-A (UVA) range: UV radiation has long been considered insignificant, due to instrument limitations and anthropomorphic oversight; it is now known to penetrate deeper into oceanic waters than was thought (reviewed by Losey et al. 1999). This observation has resulted in new efforts to understand how UVB radiation (280 to 320 nm) might affect marine organisms, and how UVA radiation (320–400 nm) is involved in visual perception (reviewed by Hessen 2003, Leech & Johnsen 2003). Collectively, a number of studies suggest that approximately half the fishes that live either near the surface or in coral reef habitats are able to see at UVA wavelengths (e.g. Losey et al. 2003).

Although it is less damaging than UVB, UVA radiation is more abundant and it can damage the retina and increase the rate of cataract formation in the lens (Meyer-Rochow 2000). Sensitivity to a wide range of

wavelengths also increases the potential for chromatic aberration, because the focal length of the lens depends on wavelength (Kröger 2000). UVA radiation, due to its lower wavelength, is also scattered more than visible light by both the environment and by the lens, cornea, and vitreous humor of the eye. This scattering decreases both image contrast and quality (Losey et al. 1999). Thus, it is generally assumed that UVA vision has adaptive functions that counterbalance these disadvantages.

Most proposed functions for UVA vision involve improved visual detection of predators and prey. While any increase in the range of wavelengths over which vision occurs can potentially improve visual detection, the UVA band has several advantages over other regions of the spectrum. First, many planktonic species are transparent at visible wavelengths, but opaque at UVA and UVB wavelengths, due to increased light scattering and presence of UV-protective pigments (Johnsen & Widder 2001). The correlation between UVA vision and predation on transparent species suggests that contrast enhancement is a relatively common use for UVA vision, although it is not universal. Indeed, the presence of both damaging UVB radiation and predators with UVA vision presents a conundrum for transparent planktonic organisms, which some species appear to solve by being opaque in the UVB (to reduce radiation damage), but relatively transparent in the UVA range (Johnsen & Widder 2001). Opaque species are also more visible at UVA wavelengths, because the background spacelight near the surface is relatively brighter in this spectral region.

UV photoreception appears to be associated with several other aspects of visual perception. In salmonids UV photoreceptors are involved in the perception of polarized light, which is used for navigation and orientation (Hawryshyn et al. 2003). In other species, they extend wavelength discrimination into the UVA (Coughlin & Hawryshyn 1994). UV vision and coloration are used by certain freshwater species for sexual signaling, and a similar use has been suggested for coral reef fishes (Cummings et al. 2003). Finally, in certain crustaceans UV radiation is a proximal cause of vertical migration (Leech & Williamson 2001, Wold & Norrbin 2004).

UVA radiation in surface waters is more variable than many other physical parameters in the ocean. Dissolved organic matter, chlorophyll and particulate matter can dramatically reduce UVA radiation levels (Hargreaves 2003). Therefore, species relying on UVA vision may be more susceptible to environmental disturbances (e.g. eutrophication, river plumes, phytoplankton blooms). Also, because UVA is attenuated more quickly than blue and green light, species that must retreat to deeper depths (e.g. due to surface tem-

perature changes) may be at a relative disadvantage, being less able to navigate and find food or mates than species relying on vision at longer wavelengths. Similarly, increased UVA radiation (due to oligotrophication or movement to shallower depths) may benefit UVA visual species. Although detrimental effects of direct exposure to increased UVB are well documented, few studies have focused on deleterious consequences mediated by increased use or effectiveness of UVA vision. Finally, while avoidance is an important defense against high levels of UVB radiation, little is known about the relationship of UVA vision to avoidance behavior.

Diel vertical migration (DVM): DVM, arguably the largest movement of animals on the planet (performed by 50% of the oceanic biomass), is visually mediated. In most cases, the ultimate cause of DVM is visual predation, and the proximal causes are diel changes in light intensity (Lampert 1993, Frank & Widder 1997). Although the depth range of vertical migration has been related to swimming speed, scant attention has been paid to the ultimate causal factor, visibility to predators at depth. The daytime depth where a species is safe from visual predation depends upon the species' depth distribution, the visual acuity and sensitivity of the relevant predators, the visibility of the animal to these predators, and the clarity of the water. While all 4 of these factors have been investigated independently, they have not been united into a predictive theory of the depth distribution of vertical migrators. Such a theory is likely to contain some non-intuitive predictions. For example, because water clarity frequently increases with depth, prey are sometimes more visible at depth, rather than less (S. Johnsen & E. J. Warrant unpubl. data).

The proximal causes of DVM have received more attention and they all appear to operate via visual control systems. Recent *in situ* research of DVM in the ocean has shown that the proximate causes vary among species (Frank & Widder 1997). Common crustacean species appear to follow an isolume, moving vertically to maintain the same subjective level of light intensity. Because it is the perceived intensity, not the measured intensity, that matters, it is necessary to measure the spectral and absolute sensitivity of the species involved. While the isolume of absolute light intensity travels too quickly at dusk and dawn for these animals to follow, the isolume of perceived intensity moves more slowly (due to spectral broadening near the surface) and can be followed by the migrating organisms (Widder & Frank 2001). Common fish species, however, do not appear to follow an isolume. Some coastal species may respond to the increased rate of change in light intensity at dawn and dusk, but this remains to be tested.

Species that follow an isolume are strongly affected by changes in surface lighting. In one case (Frank & Widder 2002) an influx of cold, turbid surface water during a DVM study lowered the light levels at depth, and the crustaceans migrated upwards to maintain their light levels (i.e. followed an isolume). After the influx had passed, they migrated downwards again. Another study of DVM in freshwater showed that light pollution reduced the range of migration (Moore et al. 2001). Finally, the daytime depth distributions of many crustaceans, and thus their migratory ranges, depend on their visual sensitivity (Frank & Widder 2002). Together, these studies suggest that anthropogenic effects on nighttime illumination, and turbidity, significantly affect the vertical distribution and migratory behavior of marine species, at least in shelf waters.

Turbidity: While it is less important in the centers of ocean basins, turbidity due to eutrophication, river plumes, dust storms, and other causes is of increasing concern in shelf waters. These impacts of terrestrial origin can extend far out into the ocean. As demonstrated in several theoretical and empirical studies in coastal and freshwater systems, turbidity significantly affects processes mediated by vision. One obvious issue is visual predation. Species that are cryptic under one set of optical conditions can often become conspicuous under different conditions (Johnsen & Sosik 2003, Johnsen 2003). Also, because increased turbidity selectively affects the visibility of targets viewed at longer distances, it affects piscivores more than planktivores (De Robertis et al. 2003, Mazur & Beauchamp 2003). Increased turbidity is also predicted to favor tactile over visual predators. Studies in Norwegian fjords suggest that turbidity is at least partially responsible for the displacement of fishes by gelatinous zooplankton (Eiane et al. 1999). These studies suggest that turbidity can drive the species composition in some marine ecosystems.

Turbidity can also influence reproductive isolation. For example, increased turbidity interferes with mate recognition in cichlid fishes of Lake Malawi by reducing the perceived contrast of their species-specific color patterns (Seehausen et al. 1997). This has led to a breakdown of reproductive isolation and to decreased species diversity. Turbidity is a serious concern also on coral reefs, but most researchers have concentrated on its (non-visual) effects on filter feeders. The bright colors of coral reef species, and their importance for mate recognition, make species diversity also vulnerable to effects of turbidity.

Areas for future research. Prevalence of photoreception in the ocean: Although many pelagic species have eyes, a larger number of species is photoreceptive without obvious ocular structures. These include many medusae, siphonophores, ctenophores,

and pteropods. Photoreception also appears to be common in single-celled plankton. Recent sequencing of the genomes of approximately 1800 microbial species from the Sargasso Sea found genes for over 782 distinct rhodopsin-like photoreceptor proteins (Venter et al. 2004). The spectral sensitivities and functions of these photopigments are unknown. Although photoreception in these species may have no visual function, it may be important for circadian and reproductive rhythms (as it certainly is for terrestrial and coastal species). For example, documenting photoreception in certain deep-sea benthic species may lead to an understanding of their well-known but poorly understood pattern of seasonal reproduction. While it has long been known that reproductive seasonality in many near-surface species is mediated by nocturnal illumination levels, deep-sea spectral irradiance measurements, and measurements of visual sensitivity are needed to determine whether this is possible in deep-sea species. More generally, a better understanding of the prevalence and functions of photoreception will allow us to evaluate the importance of light as a driving force in the ocean.

Effects of downwelling light on species distribution: As mentioned above, light levels are at least as important as other physical variables in determining the depth distributions of aquatic organisms. Modeling approaches have also suggested that visual predation has a top-down effect on the structure of pelagic ecosystems (Aksnes et al. 2004, Sørnes & Aksnes 2004). Thus, more directed investigation of the interactions of light on species distribution will be valuable. Indeed, the interactions between light and other variables that are commonly measured (e.g. temperature, salinity, depth) in determining species distribution are likely to be quite interesting. Also, because light levels are strongly affected by atmospheric conditions and turbidity, surface conditions may have a greater influence on species distribution at depth than previously considered.

Although there are excellent depth profiles of both species and light levels, they have seldom been obtained simultaneously. As mentioned above, such integration in measuring these variables is essential if progress is to be made. Although making high spectral resolution measurements of light at depth remains challenging, obtaining data on overall levels of illumination is relatively simple. Currently, 2 models of small, orientation-independent light meters (QSP – MSP, Biospherical Instruments; LI-193SA, Licor) can be connected to auxiliary data channels on a standard Seabird® CTD profiler. Given their ubiquitous use in oceanography, CTDs with light meters could add significantly to our knowledge of physical variables in the ocean for little extra cost.

Functions of bioluminescence: Given the abundance and diversity of bioluminescence, our lack of knowledge of its ecological roles is highly unfortunate. At least 80% of the pelagic species are bioluminescent (reviewed by Widder 2002). The metabolic cost of bioluminescence is high and the resulting light is conspicuous, suggesting its importance for the organism. Although confined to depth during the day, bioluminescence is ubiquitous near the surface at night, and so also affects the more commonly considered and economically important shallow water species. Counterillumination and luring with bioluminescence are relatively well understood (Widder 2002). However, other hypothesized functions—communication, mate attraction, warning signaling, blinding predators, and deterring predation by illuminating the predator or attracting higher level predators (Widder 2002)—have remained at the arm-waving stage for decades. Even the hypothesis that ocular photophores are used as searchlights is primarily supported by anatomy and common sense. Our knowledge of the bioluminescence of benthic species is particularly limited.

Functions of polarization vision: The oceanic light field is moderately polarized, and polarization sensitivity has been found in certain fishes. Behavioral and anatomical evidence suggests that it is also quite common in crustaceans and cephalopods (reviewed by Horvath & Varju 2004). Polarization vision is used for navigation, water finding, and the perception of polarized signals in coastal and terrestrial species. In marine environments, navigation by these means is only possible near the surface. Signaling may be possible for some species, but the most likely use for underwater polarization sensitivity is contrast enhancement. Silvered species, normally highly cryptic, can be detected because the reflected light is polarized (Shashar et al. 2000). Transparent species can be detected because the polarized background light can be altered by birefringence and scattering within the tissue. In addition, a recently discovered algorithm uses knowledge of the polarization of the light field to dramatically increase the contrast of images (Schechner et al. 2004). The simplicity of this algorithm suggests that it may be used by polarization-sensitive species for the same purpose. While one species of squid is known to use polarization sensitivity to enhance contrast of possible prey (Shashar et al. 1998), these questions remain mostly un-studied. As with UV radiation, underwater polarization is strongly affected by turbidity and it changes rapidly with depth near the surface (Horvath & Varju 2004). Therefore, natural and anthropogenic effects on turbidity and surface temperature (which may drive species into deeper water layers) may selectively affect polarization-sensitive species, for example by reducing predation on transparent and silvered prey. Because

polarization sensitivity can increase the range of visual detection, it may also affect the scales over which organisms can interact and forage.

Functions of novel features in the visual systems of deep-sea organisms: Anatomical studies of the eyes of deep-sea fishes and crustaceans reveal interesting features including accessory retinas, foveae, and variation in spatial acuity over the visual field (reviewed by Warrant & Locket 2004). It has been suggested that some of these features are optimizations for viewing either bioluminescent sources or dim extended scenes, but behavioral data are lacking. The visual systems of benthic species are an especially intriguing case. The eyes of deep-sea benthic species are generally larger than the eyes of pelagic species at the same depth, suggesting that there is either more to see or a greater need to see in this habitat. It has been suggested that bioluminescence is more common in the benthos than previously supposed, and that the substrate may be dimly illuminated by light from bacterial sources, but this is speculative. Understanding the visual systems of deep-sea species may provide insights into visually mediated predation and reproduction during nocturnal hours, subjects that remains poorly understood in shallow-water species.

Undisturbed observations: Terrestrial and coastal ecology have been transformed by undisturbed observations of behavior and distribution. For example, consider the state of forest ecology without data on the location, growth and shape of plants in undisturbed plots—or avian ecology without observations on mating and parental care. The lack of undisturbed observations constrains our ability to study pelagic ecology. Net capture removes almost all the information about natural distribution. Submersibles and ROVs are large, noisy, and so bright that they likely blind the species they find. Towed video arrays are being developed that use red light illumination that is invisible to deep-sea species, but these arrays have a short range and move too quickly to monitor behavior. Acoustic methods lack resolution and specificity, and are likely also intrusive. Remotely operated and baited cameras have been used at a few benthic sites, but not in the pelagic realm. Studies using blue water diving techniques cause perhaps the least disturbance, but remain uncommon and are limited to the top 30 m of the water column. Therefore, behavior is inferred from physiological measurements and the gut contents and anatomy of moribund or dead specimens. While a dead beaver with big teeth surrounded by fallen trees makes for a good argument, one would like to see the animal actually chewing on the wood.

Technical hurdles to direct, *in situ* observations of behavior of pelagic animals can be overcome. One possibility involves the use of cameras baited with

lights attached to surface and subsurface drifters. The technology for these drifters has been tested for monitoring ocean currents. Current video cameras can be quite small and draw little power and hard drives that hold gigabytes of data now hang from key chains. Lighting can draw large amounts of power, but this is not necessary at upper mesopelagic depths. Of course there are technical challenges involved in integrating cameras to the drifters, collecting the instruments or uploading the digital images via satellite, and analyzing the actual data. However, most of these problems have been solved in other contexts in oceanographic research. What is lacking is the recognition that observations of this sort are important.

Conclusions. All scientists are passionate advocates for their area of research, and visual ecologists are no exception. That having been said, it does appear that biological oceanography can reap many benefits from sensory biology. Like all fields of knowledge, oceanography requires many viewpoints. Science evolves through the push–pull dynamics of various subfields. Without this cross-fertilization of ideas, a subject can lose its vibrancy. In the case of biological oceanography, we may soon reach the point where the distribution of organisms is very well known. Physiological and behavioral knowledge of these organisms will be required to ensure that is also well understood.

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Reception before perception: how fluid flow affects odor signal encounter by olfactory sensors

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While designers might state that ‘form follows function’, and anatomists might aver that ‘form leads to function’, it is less easy to describe the relationship between form and hydrodynamics. Ecologists have given sensory biologists a plethora of examples showing how organism shapes and features are correlated with particular water flow patterns. In return, sensory biology can contribute to marine ecology by giving examples of how environmental or self-generated flows can affect function at small and large spatial scales. Since sensory signals contain information re-

quired for performing many ecologically critical activities, understanding the relationships between organismal abilities, flow, and function may lead to insights about why certain creatures thrive (or at least survive) in a particular habitat.

At the most basic level, water flow affects the properties of chemical cues that are used by many marine animals to find food, mates and habitat, to detect predators, and to communicate with conspecifics (e.g. Caldwell 1979, Ache 1982). The ability of an animal to intercept and interpret these chemical signals may depend on both large-scale (relative to the animal) environmental flows and on small-scale movements and currents generated by the animal itself. In this essay, I will explore (1) how flow affects the interception and perception of chemical signals by olfactory sensors, (2) how an animal’s ecological success might depend on the match between sensor properties and the flow habitat, and (3) how the hydrodynamics of an animal’s habitat can influence sensor morphology.

How does flow affect the interception of chemical signals? In most aquatic habitats, the downstream plume of an odor source (such as a decaying food item) consists of fine filaments of concentrated odor molecules interspersed with the surrounding fluid (Moore & Atema 1991, Weissburg 2000). The structure of the odor plume is affected by several flow characteristics, including mean current velocity, turbulence intensity, the presence of waves, and the gradient of flow speed above the substratum (Fischer et al. 1979, Crimaldi & Koseff 2001). For instance, odor filaments tend to become thinner, less concentrated, and more numerous as the turbulence intensity increases (e.g. Finelli 2000). Different substrates, such as sand, gravel or cobble, and the vegetation growing on the substrate affect turbulence intensity and give rise to different chemical signal structures (Finelli 2000, Moore et al. 2000). Therefore, fluid flow affects the properties of chemical signals in the environment.

Fluid flow can also affect an animal’s ability to encounter these chemical signals. The first requirement for olfactory perception is that the odor signals must arrive at the surface of the chemosensory sensilla. Consequently, chemosensory structures often protrude into the flow from the main portion of the body. One common example of such structures are the sensory ‘hairs’ (aesthetascs) on the antennules of most crustaceans (e.g. Ache 1982, Hallberg et al. 1992). Like any object inserted into a flow, these sensory structures are surrounded by a region of low flow, termed the boundary layer (Vogel 1994). Odor molecules such as sugars, amino acids, etc. cross the boundary layer primarily by molecular diffusion, a very slow process. Since the average time required for a small molecule to cross a boundary layer increases as the square of the bound-

ary layer thickness (Vogel 1994), this fluid structure acts as a physical filter, limiting and slowing the arrival of odor molecules at the sensors.

Aquatic crustaceans typically sample odors by flicking their antennules in a rapid out-and-back motion through the surrounding fluid (Snow 1973, Schmitt & Ache 1979, Hallberg et al. 1997). The rapid flicking helps shed old samples from the sensors and, by thinning the boundary layer, allows new odor-containing water to be sampled instead. Empirical measurements and ensuing theoretical calculations from dynamically scaled physical models of mantis shrimp antennules encountering odor filaments show that the concentration, timing of odorant arrival, rate of change of molecular flux, and the ability to take discrete odor samples are affected by sensor shape, sensor arrangement on the antennules, and antennule movement relative to the ambient water motion (Mead & Koehl 2000, Stacey et al. 2002).

Despite interspecies differences in aesthetasc morphology, arrangement, flicking velocity, and sampling axis, the flick invariably consists of alternating rapid and slow phases (Mead 1998, Mead & Koehl 2000, Goldman & Koehl 2001, Goldman & Patek 2002). Furthermore, flicking velocities are matched to the aesthetasc arrangement, so that odor filaments penetrate the sensor array mainly during the rapid stroke of the flick (Mead & Koehl 2000, Koehl et al. 2001, Stacey et al. 2002). This asymmetry of the flick ensures that the spatial pattern of odor capture by the aesthetasc array is preserved until the end of the recovery stroke, and that each flick is a discrete sample in time and space. Other mathematical models show that asymmetrical flicks can enhance the amount of fine-scale odor information potentially available to the animal, and that sensor size and speed through the water affect the likelihood that the array will detect concentrations above threshold (the probability decreases as the sensors become small or slow) (Crimaldi et al. 2002).

Functional implications of flow–sensor interactions.

As described above, the thinner the boundary layer surrounding the sensor, the more rapidly animals perceive their chemical environment. Aquatic animals employ several different strategies to thin the boundary layer surrounding their chemical sensors, and thus hasten odor acquisition. For instance, the tropical mantis shrimp *Gonodactylaceus mutatus* becomes increasingly involved in complicated aggressive and reproductive encounters as it grows. It also hunts faster and more elusive prey. These complex social and foraging behavior patterns require rapid responses. Perhaps to accommodate the need for speed, antennule flicking velocity increases several fold with body size (Mead et al. 1999), reducing the boundary layer so that odors penetrate the array more quickly (Mead & Koehl 2000).

Similarly, male copepods (*Temora longicornis*) swim about 5 times faster than females when 'mate-tracking' along short-lived odor plumes created by swimming females (Doall et al. 1998, Weissburg et al. 1998). This high swimming speed may be necessary to enable the odor trail information to penetrate male copepod sensory arrays, so that the male can follow the trail before it and the female disappear. In addition, crayfish in stagnant lakes create their own currents using fan organs (Breithaupt 2001). One function of these self-generated currents may be to draw in odor-laden water at a velocity high enough to decrease boundary layer thickness and allow odorants to contact the sensor array.

However, thick boundary layers may pose advantages as well. Most of the odor filament sweeps by the sensor without being sampled when the boundary layer is very thin. A thicker boundary layer increases the sample volume around that sensor even though it increases the time needed to detect an odor filament. If response speed is unimportant, animals with a small sensor surface area (few sensors or small sensors) might maximize olfaction by flicking more slowly and allowing the boundary layer to be thick, as this will increase the sampling of odor molecules. Small, immature *Gonodactylaceus mutatus* hunt slow prey and engage in less social behavior as their larger relatives. These small mantis shrimp sweep their antennules relatively slowly and infrequently. This sampling protocol allows more of the molecules captured within the boundary layer time to diffuse to the sensor surface before the sample is shed by the next flick. Encountering a larger proportion of the odor molecules in a given sample may enable the mantis shrimp to detect very dilute odors (Mead et al. 1999).

Ecological implications of flow–sensor interactions. By affecting either odor plume structure or its interception, environmental or self-generated flow could influence any aspect of the animal's ecology that relies on accurate olfaction. For instance, flow might influence foraging effectiveness by affecting the signal structure of odors emanating from a food source. Behavioral observations in a variety of animals highlight such effects. Blue crabs are more successful and efficient at finding odor sources when flow speed, and hence turbulence, decreases (Weissburg & Zimmer-Faust 1993, Finelli et al. 2000). Interestingly, enhanced turbulence is not always detrimental. Crayfish find odor sources more efficiently on a cobble substrate rather than on sand (Moore & Grills 1999). Knobbed whelks find food odor sources equally well regardless of ambient turbulence (Ferner & Weissburg 2005). Similarly, the ability of stomatopods to find odor sources increases when waves are superimposed on unidirectional flow (Mead et al. 2003). Flow habitats

therefore vary in their ability to support the use of chemical signals. By inference, certain flow environments may not allow for the establishment of strong chemical signals or for their interception by the tracking animal's sensors. Low food uptake may compromise growth rate (Shaffner & Anholt 1998) or reproductive output (Gliwicz 2001) if foraging efficiency is decreased as a result of poor sensory performance. If time spent foraging increases to compensate for low foraging efficiency, as seen in some terrestrial herbivores (Owen-Smith 1994), greater vulnerability to predators might increase mortality.

Differences in how flow delivers mating cues also could affect an individual's mating success. Nothing is currently known about whether there are individual differences in the 'attractiveness' of mating cues used by aquatic organisms, or in the sensitivity of such cues to changes in water flow. Certain individuals might theoretically produce especially high concentrations of mating cues. These cues might be less sensitive to the diluting effects of turbulent flow, and thus might elicit tracking responses in a greater number of potential mates than cues emitted at lower concentrations, from a subsequently less attractive mate.

In many crustaceans, individuals that have been opponents in aggressive encounters can recognize one another via chemicals contained in released urine, and aggressive encounters with the same individual can thereby be avoided (e.g. Zulantz Schneider et al. 2001). If these cues are not transmitted or received effectively, the number of aggressive encounters would rise, resulting in greater damage and mortality.

Many aquatic animals also rely on chemical cues to find a suitable habitat. For larvae with a limited time window for settlement and/or limited settlement areas (e.g. marine larvae searching for particular reef environments) mortality could be affected by changes in flow conditions. For instance, the number of larvae that swim downward in response to settlement cues depends upon the flow speed (Tamburri et al. 1996), as does the overall pattern of larval motion (Pasternak et al. 2004). In some cases, the habitat cue is an extremely diverse chemical cocktail (Hadfield & Paul 2001). As discussed above, highly concentrated or potent cues might be relatively protected from the diluting effects of turbulent flow. These cues are likely to be more effective than others when flow is turbulent. Thus, the selective impact of flow-related dilution effects on chemical signals potentially alters species distributions and the survival of individuals, by affecting their ability to obtain accurate information about their biotic or abiotic surroundings.

Why might chemosensory arrays be tuned to a particular hydrodynamic habitat? Since features such as freestream velocity, turbulence, the presence or

absence of waves, and substrate roughness affect chemical signal features, it is likely that certain arrangements of olfactory sensors will be most efficient at detecting particular types of odor signals, or odor signals in particular habitats. Antennal design in the sphinx moth represents an example of sensor 'tuning' via the physical filter imposed by a particular morphology. In this animal, the different shapes of male and female antennae appear to heighten signal characteristics relevant to odor plumes of interest to that gender (e.g. males respond to a point odor source of a calling female on a branch; females respond to the much larger odor source of a field of flowers; Schneider et al. 1998). Analogous examples for aquatic organisms are scarce, but there is some evidence that crayfish antennules may be tuned to their flow habitat. For instance, crayfish appear to exhibit flow-related differences in sensor length relative to the boundary layer created by the filament supporting the sensors (K. S. Mead unpubl.). Sensilla that are long relative to the antennule filament will be better able to protrude past the boundary layer and will thus facilitate odor sampling. Since the boundary layer created by the filament is thicker in low flow, one might predict that animals that rely on rapid olfactory information in calm habitats will have longer olfactory sensilla relative to the filament diameter than animals from habitats experiencing stronger currents. Measurements of antennule diameters in large reproductive individuals from 3 species of *Cambarus* and 3 species of *Orconectes* occupying 3 flow regimes (ponds, streams with mean current velocity $<5 \text{ cm s}^{-1}$, and streams with mean current velocity of $\leq 30 \text{ cm s}^{-1}$ in early summer) reveal that sensilla were 13% longer relative to filament diameter in animals from habitats experiencing the lower mean flows (K. S. Mead unpubl.). The similar comparison among small, non-aggressive, non-reproductive animals that do not depend on rapid olfactory information has not been done, but the relationship between flow and relative aesthetasc length would not be expected if the 'need for speed' is restricted to adults.

Flow might alter the optimal density of crayfish sensory structures in predictable ways. Receptive surface area increases with receptor density. Thus, there would be a selective advantage to packing in the maximum number of sensilla per unit length, provided that crowding does not adversely affect odorant access. Physical and mathematical modeling of stomatopod aesthetascs has shown that packing sensilla close together can inhibit odorant access to the sensor surface unless the sensor is moved through the surrounding fluid rapidly to reduce the boundary layer (Mead & Koehl 2002, Stacey et al. 2002). Rapid environmental flows should facilitate odorant penetration of the sensor array as easily as does rapid antennule movement.

Foraging in strong currents may permit sensory arrays to be more tightly packed than in still water, and this would increase sensor density and improve sampling ability.

Some evidence suggests that flow habitats affect the structure of the sensory array. In crayfish and some other crustaceans, aesthetascs are organized into 2 bundles per antennule annulus. A good measure of the 'crowdedness' of an array is the ratio of the gap between adjacent bundles of sensilla and the diameter of each sensillum. This 'gap:diameter ratio' has been used to model the ability of odor-containing fluid to penetrate a sensor array (Cheer & Koehl 1987, Koehl 1995). Because aesthetasc diameter increases with body size, it is appropriate to normalize gap:diameter ratios by body size. Among the 6 crayfish species measured to date, the gap:diameter ratios relative to rostrum–telson length are 30% greater in the high flow species than in the low flow species, supporting the concept that increased sensor packing allows animals to maximize olfactory sampling in rapid flow environments. (K.S. Mead unpubl.). This view is further supported by Ziemba et al.'s (2003) study comparing antennule structure in a surface and a cave-dwelling crayfish (*Orconectes cristavarius* and *O. australis packardii*). The cave-dwelling species, which experiences lower average flow, has longer antennules and longer aesthetascs. The surface species, which experiences higher flow on average, has more aesthetascs per unit length than the cave-dwelling species (gap:diameter ratio was not reported).

Ecological implications of biomechanical tuning. If sensory arrays are designed to enhance particular signal features, or to work well in particular environments, then there is the possibility that they will work less well in other environments. And yet, some aquatic organisms occupy a range of habitats. There are several scenarios that might explain this apparently anomalous observation: (1) Some combinations of strong chemical signals, sampling strategies, and navigational algorithms may be so successful that they are not greatly influenced by flow. (2) The physiological 'margin for error' may be great enough so that the animal's ability to use the odor signal effectively is not compromised, or low success rates may be tolerable. (3) Some animals may be able to compensate for changes in flow conditions, much in the way that many filter feeders (such as barnacles) change their feeding movements, postures, and even morphology in response to the flow environment (Li & Denny 2004). For instance, molting may provide an opportunity for remodeling body shape. Crustaceans also may be able to control sampling by altering the flicking velocity and the attendant physical filtering properties of the

array (such as boundary layer thickness) even if morphology remains fixed. Feedback loops from mechanosensors on the antennules conceivably could report on both antennule velocity relative to the surrounding fluid, or some indicator of boundary layer thickness, to facilitate these changes.

Few studies have attempted to separate the influence of hydrodynamically induced changes in sensory performance relative to the multiple factors that affect an organism's distribution. Thus, it is unclear whether a broad species distribution is based on flexible odor sampling strategies, even in species that occupy a large geographic or environmental range. However, it may be possible to identify sensory specialists and generalists, and to determine whether the ability to alter either sensory structures or sampling strategy is correlated with the ability to thrive in habitats with different hydrodynamic characteristics.

Directions of future research. Although progress has been made regarding how water flow affects odor signal encounter by olfactory sensors, there are still many questions left unanswered. How universal is the sampling volume asymmetry (e.g. flicking) seen in some crustaceans? Do animals use different sampling strategies according to their mode or speed of locomotion? Do animals sample differently as a function of temperature-induced changes in viscosity? Does odor penetrate sensor arrays only when the appendages bearing the arrays move through the flow, or are there circumstances under which stationary receptors would have access to odors? What is the effect of flicking along a vertical axis vs along a horizontal axis (relative to the substrate), or of using other patterns of movement? Are there fundamental differences between sampling of odors in a wave regime or in a unidirectional flow? In addition, male–female differences in sensor morphology, arrangement along the antennule, and antennule flicking remain to be explored. These male–female differences are not universal, but are present in some species with sex-specific behavior (Hallberg et al. 1992). Are these differences in structure and behavior also related to the occupation of slightly different microhabitats?

Although there are currently no answers to these questions, some hypotheses can be formulated as guides for future research. One postulate is that most crustaceans will be found to employ asymmetric flicks because flick asymmetry ensures that samples are discrete in time and space. I would also predict that crustaceans will alter their flicking regimes as the flow environment changes. As current velocity increases, an animal might alter the relative speeds of the outward and return parts of the flick. This might help the animal maintain the asymmetry of its flick so that each flick samples new water. Since visco-

sity increases substantially as temperature decreases (Vogel 1994), I would expect antennule velocity to be disproportionately high in crustaceans in cold water to compensate for the increased boundary layer thickness.

So far, I have discussed approaches from behavioral experiments, biomechanics, and chemical ecology to show how fluid flow affects signal encounter through the surface of the sensory array. However, to fully understand how flow affects sensory biology and the ecological activities that rely on accurate chemical information, it is also necessary to consider how the structure and arrangement of the olfactory receptor neurons might affect odor signal reception and perception. For instance, among arthropods, the number of sensory cells innervating sensilla is species specific (Hallberg et al. 1997). Given that each sensillum has a limited internal volume, a small number of cells would seem to favor greater sensitivity to a limited number of odorants, whereas a large number of cells might enable the animal to respond to a greater number of odor molecules (Ziemba et al. 2003). One could imagine that, along with changes in external structure, the number of olfactory sensilla might increase as an animal grows, experiences new olfactory requirements, and possibly an increased need for rapid responses. This appears to be the case in at least some decapod crustaceans, in which the number of aesthetascs and the number of innervating sensory neurons increase with size. At least in crayfish, these additions seem to enhance sensitivity, rather than increase the suite of stimulatory odorants (Beltz et al. 2003 and references therein). Future exploration of these issues should consider whether innervation, either by different numbers of sensory cells or sensory cells with different response characteristics, is correlated with fluid flow.

New technologies will also be required to evaluate the relationship between chemosensory performance and ecological properties. Potentially valuable techniques include planar laser-induced fluorescence (PLIF), which enables the measurement of detailed odor filament characteristics (e.g. Crimaldi & Koseff 2001), and microarray electrodes that allow ensemble recording from populations of cells that process chemosensory signals in behaving animals (Daly et al. 2004). These advances will contribute to our understanding of the timing and content of the chemical signals encountered by animals and of the way in which the animals use the information contained in the chemical signals to track odor plumes, settle, or otherwise conduct their daily activities. Even without these tools, important contributions can be made by behavioral ecologists and other specialists. We need more detailed information about the life histories of

plume tracking animals, so that we may understand which environmental flows they experience during different life stages. Ultimately, by combining precise laboratory experiments and realistic field observations, these efforts will increase our understanding of the complicated interaction between an organism and its flow environment. Then we can begin to appreciate how this interaction shapes the ongoing chemical 'conversation' between an animal and its surrounding world.

Adaptations of the fish lateral line for the analysis of hydrodynamic stimuli

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Water motion provides a wealth of sensory information in the aquatic world. To use this information, aquatic animals have evolved highly sophisticated hydrodynamic receptor systems (Bleckmann 1994). Fishes detect hydrodynamic stimuli with the lateral line, a sensory system that was initially described as 'touch at a distance' (Hofer 1908, Dijkgraaf 1963). With their lateral line system, fishes detect and analyze relative movements between their bodies and the surrounding medium at each of up to several thousand receptive units, termed neuromasts, that are distributed across the fish's body.

A neuromast consists of a patch of sensory hair cells that are similar in function and morphology to those in the auditory and vestibular system of vertebrates. The hair cells are covered by a gelatinous dome-like structure, the cupula. Water movements cause the cupula to slide across the sensory epithelium (van Netten & Kroese 1987) resulting in shearing motions of the hair bundles and a consequent change in the hair cells' membrane potential.

The peripheral morphology of the lateral line is highly variable among fish species (Webb 1989). Concurrently, the hydrodynamic environments in which fishes live are highly diverse both in terms of background noise and stimuli that are detected by the lateral line. This has led to the hypothesis that the design of the peripheral lateral line represents an adaptation to the hydrodynamic conditions that prevail in the habitat of a given species and/or the species' life style. The intent of this article is to demonstrate how lateral line design is connected to fish ecology and to discuss possible adaptations of the lateral line to sensory stimuli.

Peripheral lateral line subsystems. The most obvious feature of the lateral line is that it consists of 2 morphologically and physiologically different subsystems, the superficial neuromast (SN) and the canal neuromast (CN) systems. Functionally, SNs are velocity detectors, i.e. their responses are proportional to the velocity of external water motion. CNs, in contrast, are pressure gradient detectors, i.e. they respond to pressure differences between canal pores (e.g. Coombs & Montgomery 1998). The adaptive significance of these 2 systems has recently been revealed in neurophysiological experiments demonstrating that nerve fibers innervating SNs exhibit increased activity in a laminar water flow whereas nerve fibers innervating CNs do not respond to water flow (Engelmann et al. 2000, 2002, Voigt et al. 2000, Carton & Montgomery 2002). The disparity between responses of CNs vs. SNs is due to the fact that in flowing water, SNs are continuously stimulated, whereas CNs are not stimulated since the flow does not create appreciable pressure differences between canal pores. As a consequence, neural responses of SNs to sinusoidal water motions are masked by water flow, whereas CNs represent sinusoidal water motions both in still and flowing water (Engelmann et al. 2000, 2002). These findings suggest that many superficial neuromasts represent an adaptation to still water conditions, whereas a well-developed canal system, but only few superficial neuromasts, may be an adaptation to flowing water conditions. In agreement with this hypothesis, fishes that live in flowing water, or that are fast swimmers, tend to have extended lateral line canals and canal specializations (e.g. canal branchings) but few superficial neuromasts. In contrast, species that live in still water and are slow swimmers or have sedentary behavior often have reduced, simple canals and a large number of superficial neuromasts (Dijkgraaf 1963, Marshall 1971, Bleckmann & Münz 1980, Vischer 1990). In addition, many fishes with an abundance of superficial neuromasts have body shapes that are not appropriate for fast swimming, e.g. deep-sea anglers and elongate gulper eels. However, there are exceptions to these trends. In gobies, for instance, most of the canal neuromasts are replaced with superficial neuromasts (Miller 1986), yet gobies are frequently found in rivers. Perhaps gobies and other freshwater-tolerant species occupy vacant freshwater niches where lateral lines that are well adapted to flowing water are unnecessary. It also may be possible that the fish live in microhabitats where flow is greatly reduced, e.g. in small pools, behind obstructions, or in burrows.

The differences in form and function between the superficial and canal systems suggests that they are used in different behavioral contexts. Behavioral studies indicate that in a number of species the SN (but not

the CN) system, is essential for rheotaxis, i.e. the orientation to bulk water flows. Rheotaxis is a prerequisite for a number of behavioral patterns, for instance in following odor trails or holding station in a flow. Destruction of the SN system increases the threshold for rheotactic behavior, whereas elimination of the CN system has no such effect (Montgomery et al. 1997, Baker & Montgomery 1999). The high-pass filtering characteristics of the CN system, in contrast, may underlie detection and localization of oscillatory signals in flow. Mottled sculpin *Cottus bairdi*, a benthic species with few SNs, can detect and localize relatively weak sinusoidal signals in the presence of background flows of up to 8 cm s^{-1} . Detection thresholds in flow are increased only 2 to 4× compared to the threshold in still water (Kanter & Coombs 2003).

Adaptations to biotic hydrodynamic stimuli. The various morphological patterns of the peripheral lateral line may in part reflect adaptations to particular hydrodynamic stimuli that are relevant to the daily lives of fishes. Perhaps the most clear-cut example is the lateral line of surface-feeding fish. Species like the topminnow *Aplocheilichthys lineatus* and the African butterfly fish *Pantodon buchholzi* detect water surface waves caused by prey (e.g. terrestrial insects that have fallen into the water), and can precisely localize target angle and distance (Bleckmann et al. 1989). Prey-generated surface waves last for several seconds, have displacement amplitudes below $100 \mu\text{m}$ peak-to-peak, and an irregular time course with frequencies above 50 Hz. Wind-generated surface waves, in contrast, may have displacement amplitudes of several cm but do not include frequencies above 10 Hz (Bleckmann 1994). The cephalic lateral line of surface-feeding fish is highly adapted to detect surface waves. It consists of 6 rows, each containing acceleration-sensitive neuromasts that are well suited to detect high-frequency signals against low-frequency background noise (Bleckmann et al. 1989).

In contrast to the highly specialized cephalic lateral line of surface-feeding fish, lateral line adaptations to subsurface water waves are less well studied. One noticeable exception is the blind cave fish *Astyanax mexicanus*, a cave-dwelling still-water species without eyes. When swimming and gliding, *A. mexicanus* generates a flow field around its body and uses its lateral line to obtain information about stationary objects in its vicinity by perceiving patterns in the flow field around its body. The flow fields on both sides of the body are equal in the absence of nearby objects. However, when the fish passes an obstacle, the flow field on the side that faces the object is altered and the lateral line experiences an increase in water velocity and pressure changes that travel over the fish's body (Hassan 1989). This information can be used by the blind cave fish to

avoid obstacles (von Campenhausen et al. 1981) and to discriminate between pairs of grids that differ in spacing by as little as 1.25 mm (Weissert & von Campenhausen 1981). The lateral line of *A. mexicanus* consists of numerous SNs in addition to a well-developed canal system (Grobbe & Hahn 1958). The cupulae of the SNs are much longer than those in the sighted form of *A. mexicanus*, an adaptation that may improve the functioning of the lateral line and compensate for the lack of vision (Teyke 1990). After destruction of the canal system, blind cave fish reduce their swimming velocity, avoid swimming along a wall and can no longer discriminate a surface with a grid pattern from a smooth surface (Abdel-Latif et al. 1990). This suggests that they use input from their canal system to analyze hydrodynamic information that arises from alterations of the self-generated flow field. Interestingly, the ability of the cave fish to detect and approach a small sinusoidally vibrating sphere is not affected by destruction of the CN system. Thus, at least under still water conditions, *Astyanax* can find an oscillating object by means of its SN system. Presumably, all species with a fairly straight trunk canal system should be capable of imaging their surroundings like the blind cave fish, but this requires further investigation. It is also not known how imaging with the lateral line in *Astyanax* and other species is disturbed by background flow. However, from the above notions one would expect that a laminar flow does not substantially affect CN-mediated hydrodynamic imaging.

How the lateral line is adapted for the detection of subsurface stimuli generated by prey or conspecifics is largely unknown. Swimming animals generate hydrodynamic stimuli that range from short-lasting and transient, to long-lasting and oscillatory, or may be a mixture of both (Bleckmann 1994). Zooplankton organisms such as ostracods and amphipods generate oscillatory water motions that contain strong frequency components in the 10 to 40 Hz range (e.g. Montgomery 1989). In some Antarctic fishes, the frequency sensitivity of the anterior lateral line matches the frequency range of zooplankton-generated signals (Montgomery & Macdonald 1987). Interestingly, the frequency response characteristics are remarkably similar in different species despite differences in lateral line morphology, indicating that comparable tuning properties can be achieved with different peripheral designs (Montgomery et al. 1994). It is presently unclear whether other fishes display well developed correlations of lateral line frequency responses to prey frequency signatures. However, the general existence of such correlations would permit a prediction of suitable prey properties based on an analysis of lateral line function.

Fishes employing sub-undulatory swimming generate a trail of vortices (Bleckmann et al. 1991, Blickhan

et al. 1992) that persists for several minutes, representing water disturbances that might be sensed by piscivorous predators (Hanke et al. 2000). Moreover, the hydrodynamic trails produced by species with different swimming styles differ in their spatial and temporal extent. As Hanke & Bleckmann (2004) showed, the wakes generated by swimming *Lepomis gibbosus* and *Thysochromis ansorgii* have a greater lateral spread than the wake produced by *Colomesus psittacus*. Whereas *L. gibbosus* and *T. ansorgii* produce undulatory swimming movements, lateral tail flicks and pectoral fin movements, *C. psittacus* mainly uses a tetraodontiform swimming style, i.e. dorsal and anal fin undulations. Consequently, the *C. psittacus* trail shows one narrow zone of water disturbance whereas the trails of the 2 other species divide in 2 or more branches. In addition, the water velocities produced by *C. psittacus* are lower than those generated by the 2 other species. Presumably, predatory fish species use their lateral line to detect, identify and follow the hydrodynamic trails generated by prey fishes; catfish, for instance, followed the hydrodynamic trails generated by a guppy that served as prey (Pohlmann et al. 2001). Even though the spread of the hydrodynamic trail and the associated water velocities depend on fish size, swimming style and velocity (Hanke & Bleckmann 2004), the spatio-temporal scale for hydrodynamic trail following may be quite large. A fish such as *L. gibbosus*, which swims with undulatory body movements at a speed of 0.4 m s^{-1} covers a range of 24 m in 1 min, i.e. a distance over which vision and hearing are limited, if not useless. On the other hand, after 1 min the hydrodynamic trail of a fish still consists of water velocities well above the detection threshold of the lateral line.

The lateral line of predatory fishes such as sharks and perch is still poorly studied with respect to adaptations to prey-generated signals. Moreover, it is difficult to speculate about morphological and functional adaptations of the lateral line of predatory species without detailed knowledge about the spatial and temporal patterns and the frequency characteristics of the stimuli generated by their prey. Nevertheless, the analysis presented above suggests that piscivorous fish may require specific lateral line properties, and in this respect they may be considered specialists since their lateral line system, like other senses, must be tuned to prey-generated signals. Even though the relative importance of SNs vs. CNs for predation probably varies between species, some basic predictions can provide useful guidelines for future research. Predators will, in most cases, detect prey-generated signals head-on, predicting a well-developed head lateral line. For instance, the stargazer, a sit-and-wait predator, detects the hydrodynamic trail generated by a

moving object passing its head most likely with the neuromasts in its mandibular canal (Montgomery & Coombs 1998). Long distance detection (e.g. 10s to 100s of cm) of even large prey requires that predators need to be sensitive to minute water velocities. After 1 min, the hydrodynamic trails of swimming fish still contain water velocities of about 1 mm s^{-1} and, these velocities fall to about 0.5 mm s^{-1} after 5 min (Hanke & Bleckmann 2004). Lateral line sensitivity can also be increased in fishes by a proliferation of SNs, like in the round goby *Neogobius melanostomus* (e.g. Marshall 1986), or by the presence of wide membraneous canals (because such canals reduce laminar flow noise), as in ruffe (Janssen 1997). To analyze and distinguish between prey-generated vortices, the lateral line of predatory fish must have a spatial and temporal resolution that matches or is finer than the spatio-temporal extent of the vortices. Finally, the predator's lateral line should be most sensitive to the range of frequencies associated with prey-generated vortex rings. Physiological data that would support these latter predictions are not at hand.

Adaptations to abiotic hydrodynamic stimuli. The water motions generated by abiotic sources are often considered to constitute hydrodynamic noise that interferes with the detection of other relevant stimuli, such as those generated by prey or mates. However, abiotic sources may in some cases provide important sensory information. For instance, ocean currents, tides, river flows, wind, temperature, salinity gradients and gravity generate large scale water motions (Wetzell 1983) that may be used in fish orientation. As already pointed out above, orientation in laminar water flows is most likely mediated by the SN system (Montgomery et al. 1997, Baker & Montgomery 1999). Turbulent flows are caused, for instance, by obstacles in flowing water. Brook trout *Salvelinus fontinalis* are capable of orienting non-visually behind objects in streams (Sutterlin & Waddy 1975). Recently, Liao et al. (2003) showed that trout zigzag with reduced muscle activity between experimentally generated vortices, thus decreasing the costs of locomotion compared to undulatory swimming. Presumably, trout sense the vortices with their lateral line system. Compared to still water species, trout have only few SNs on their body (Engelmann et al. 2002) and this is thought to be an adaptation to flowing water. Thus, they most likely sense vortices with their well-developed canal system. In fact, cutting the posterior lateral line nerve, i.e. the nerve that provides the sensory input from the trunk lateral line, reduces the ability of trout to hold station behind obstacles (Sutterlin & Waddy 1975).

Perspectives. The lateral line systems are perfectly suited for studying how sensory systems have been shaped in the course of evolution to match the fishes'

sensory needs. However, we are still far from a complete understanding of lateral line sensory ecology. We need better descriptions of the water motions generated by prey, predators and conspecifics, and of the background noise conditions that fishes experience, to be able to correlate lateral line morphology and physiology to the physical environment. These data must be compared with careful descriptions of the life styles and the peripheral lateral line designs of species that live within certain hydrodynamic environments, including information about number, size, form and location of superficial and canal neuromasts, and sizes, locations and branching patterns of canal systems. In addition to this descriptive information, behavioral and neurophysiological studies with species from various habitats, exhibiting different lateral line morphologies and life styles need to be conducted under various noise conditions, i.e. laminar and turbulent flows. This will help to uncover systematic relationships between lateral line design, function and the animals' sensory needs and thus contribute to our understanding of the interplay between ecology and sensory biology of the fish lateral line.

Seeing the world through the nose of a bird: new developments in the sensory ecology of procellariiform seabirds

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Background. Procellariiform seabirds (petrels, albatrosses and shearwaters) have been a wonder to sailors and biologists for many hundreds of years. These long-lived birds spend nearly all of their lives in flight over the ocean, and are tied to land only for a few months each year (or every other year) to breed and rear a single offspring. They typically nest on isolated islands, either in burrows or above ground, depending on the species. Adults forage offshore on a variety of patchily distributed prey types and return periodically to provision the nestling (reviewed by Warham 1990, 1996). Amazingly, these foraging trips are often hundreds or thousands of kilometers from the breeding colony. How they so casually perform such miracles of navigation is not well understood.

As sensory ecologists, our approach to this problem has been to integrate sensory data with detailed

knowledge of life history, diet, and atmospheric chemistry to better understand the foraging behavior of a well-described assemblage of Southern Ocean procellariiform seabirds. Results show that olfactory foraging operates at different spatial scales, and that different species use distinct sensory strategies for exploiting prey. In parallel, we are investigating how different species use sensory cues to relocate their individual nest sites in remote breeding colonies. The emerging picture suggests that early life history can be used to predict the sensory strategies that a species expresses later on in life with respect to both foraging behavior and nest relocation.

Overview of foraging. Nevitt (2000) has suggested that procellariiforms use odor cues at 2 spatial scales: (1) At large spatial scales (1000s of square km), procellariiforms may use changes in the olfactory landscape to recognize productive areas where prey are likely to be found (Nevitt et al. 1995). In support of this idea, Nevitt and coworkers demonstrated that procellariiform seabirds could detect dimethyl sulfide (DMS), a sulfur-based compound released from phytoplankton. Emissions become elevated in surface seawater associated with oceanic features such as upwelling zones and shelf waters where procellariiforms typically forage. (2) Once an individual has arrived at a productive area (10s or 100s of square km), the problem becomes one of locating exploitable prey patches. Thus, a change in the large-scale olfactory landscape may trigger a bird to begin a small-scale area-restricted search of the region using a combination of visual, olfactory, and other sensory cues to pinpoint a prey patch. Some species may zigzag upwind to focus activity near the source of an odor plume, whereas others rely more heavily on visual cues provided by the prey items themselves or by aggregations of other foraging seabirds and marine mammals (Silverman et al. 2004).

With respect to locating prey by smell, different species of procellariiforms are sensitive to a variety of nat-

ural, scented compounds associated with prey. These include fishy-smelling odors, scents emitted from macerated krill, as well as biogenic sulfurous compounds associated with phytoplankton and krill (see discussion in Nevitt et al. 2004). Attraction to the following odors has been reported for approximately 20 species of procellariiforms: krill (crude extract, trimethyl amine, pyrazine, 2,3-dimethyl pyrazine), squid, cod liver oil, herring oil, and phenyl ethyl alcohol (a non-food related rose scent). Although there is a loose correlation between prey type and odor preferences of certain species, we have been surprised to find that attraction to odors does not necessarily correlate to preferred prey (Table 2). For example, some species that forage predominantly on krill are not attracted by krill extracts in experimental trials. Instead, these species actively track DMS, which is released by phytoplankton during grazing by krill (Nevitt et al. 1995, Nevitt 1999a). Other species will not track DMS in experimental trials but can easily be lured to krill extracts and derivatives of krill (pyrazine, for example).

Species-specific foraging strategies. We are now beginning to define how patterns of olfactory sensitivity are linked to other adaptations and developmental life history strategies. Towards this end, we have identified 2 distinct sensory-based strategies for locating prey at small spatial scales, corresponding to 'early detector' and 'late detector' strategies (Nevitt 1999b, Nevitt et al. 2004). DMS is likely to be released as krill aggregate near the ocean surface to graze on phytoplankton. Birds that are highly responsive to DMS (i.e. storm petrels and prions) may detect this early cue and locate the prey patch using an olfactory search strategy. Thus, these early detector species capitalize on the local DMS emissions to become the first to exploit the prey resource. Once the early detectors have located a prey patch, the types of cues available to other foraging seabirds change. For example, with feeding, odors from macerated krill are released. In addition, the physical presence of the early detectors

Table 2. Odor responses to DMS (dimethyl sulfide) and dietary preference in 9 species of Antarctic procellariiformes. +: positive response; -: no difference in response to experimental and control slicks or aerosols (compiled from Nevitt et al. 2004)

Common name	Species	Krill in diet (%)	DMS	Nest type
Blue petrel	<i>Halobaena caerulea</i>	75	+	Burrow
White-chinned petrel	<i>Procellaria aequinoctialis</i>	47 to 59	+	Burrow
Black-bellied storm-petrel	<i>Fregetta tropica</i>	5	+	Burrow
Prion (unidentified)	<i>Pachyptila</i> sp.	1 to 87	+	Burrow
Wilson's storm-petrel	<i>Oceanites oceanicus</i>	40 to 85	+	Burrow
Black-browed albatross	<i>Diomedea melanophris</i>	35 to 39	-	Surface
Wandering albatross	<i>Diomedea exulans</i>	10	-	Surface
Giant petrel (unidentified)	<i>Macronectes</i> sp.	5 to 33	-	Surface
Cape petrel	<i>Daption capense</i>	2 to 85	-	Crevice

provides a visual cue to the location of the prey patch. These multimodal stimuli draw in late detector species via visual or behavioral cueing (see Silverman et al. 2004). In some cases, late detectors aggressively dominate the rapidly growing mixed-species feeding aggregation, forcing out smaller early detector species (storm-petrels) that may already be satiated. Thus, for some species, olfaction provides an early detection system for opportunistic foraging, either on small patches, or on larger patches before other birds arrive. Other late detector species employ a multimodal foraging strategy that relies more heavily on visual than olfactory cues to locate prey.

Most intriguingly, birds exploiting different foraging strategies also share certain morphological and life history characteristics. As Table 2 indicates, early detectors frequently nest in burrows that can be as deep as 2 m underground (reviewed by Warham 1990). These species also seem to be designed to avoid being detected both at sea and on land: they are cryptically colored, typically fly within a meter of the ocean surface, and enter colonies at night. They also tend to immediately perform zigzag search behaviors when presented with prey odors, even when other birds are present (Nevitt 1999b). Late detectors, on the other hand, are highly conspicuous both at sea and on land and are less vulnerable to predation. These species nest in shallow crevices or above ground, and their size and contrasting coloration makes them more visible at sea. They routinely enter colonies in broad daylight, and frequent large, mixed-species feeding aggregations. These birds can have a more varied diet, which can include smaller species of petrels (see discussion in Nevitt et al. 2004). Early detectors are adapted to a 'get in and get out quickly' foraging strategy that minimizes interactions with competitors. In contrast, late detectors seem to be better equipped for exploiting prey under competitive conditions.

Development of foraging strategies. It would appear that early detectors and late detectors have developed different strategies for exploiting prey, but how are these foraging strategies linked to life history? More specifically, is there anything about the burrow environment that is conducive to developing a heightened sense of smell? Although other pelagic seabirds spend months tutoring their offspring, procellariiform chicks fledge and survive the open seas without aid or instruction from a parent (Warham 1990). Since olfactory foraging is particularly critical for burrow-nesting species, we are beginning to investigate whether chicks reared in burrows learn odor cues before leaving the nest. In support of this idea, it is well established that olfactory sensitivity is physiologically tuned after birth in a variety of animals. In some cases, this tuning has been linked to behavioral preferences for

particular foods, or other aspects of life history and ecology (reviewed by Hudson 1999). To explore this idea with procellariiforms, we need to better understand how early rearing condition impacts sensory development, both proximately and in an evolutionary sense.

Several burrow-nesting species are responsive to odors as chicks (e.g. De Leon et al. 2003, Cunningham et al. 2003). Moreover, petrels are themselves rather redolent birds, and sometimes retain odors associated with phytoplankton, fish or krill on their plumage when returning to the colony (G. A. Nevitt pers. obs.). This observation suggests that odors brought back on the feathers of parents might be detected by chicks, and thus provide the means to learn odors associated with prey even before chicks leave the nest. Moreover, compared to ground nesters, smell is likely to be a primary sensory stimulus during the first few months of a burrow-nesting chick's life. It is well known that sensory input and deprivation can influence the functional development of sensory systems (this is often overlooked by foraging ecologists). Among the procellariiforms, we do not know whether sensory systems develop differently in burrow or ground nesters. These are intriguing questions, worthy of further exploration.

Finding the nest by smell. We are only beginning to appreciate the complexity of the other great sensory challenge that petrels and albatrosses are faced with: homing back to their colony, and finding their own nest site. The model for olfactory navigation in landscapes that has been formulated for foraging behavior could easily be extended to other types of orientation at sea. For example, an odor landscape superimposed upon the ocean's surface that reflects stable oceanic features, such as shelf breaks or seamounts, could provide birds with a set of navigation cues for relocating the colony (Nevitt et al. 1995, Bonadonna et al. 2003a). However, like other animals, procellariiforms are likely to use a hierarchy of cues to relocate their colonies. This complicates our ability to identify which cues are commonly used, since birds are probably able to switch between sensory modalities, depending on environmental conditions or the manipulations imposed upon them by experimenters (Benhamou et al. 2003, Bonadonna et al. 2003c).

Once birds have arrived at the colony, most species that use olfaction to forage also rely on smell rather than vision for relocating their own nest sites (Bonadonna & Bretagnolle 2002). It is now well established that the characteristic smell of an individual's burrow assists the returning bird in quickly and efficiently relocating its nest site from among hundreds of others, at night and under heavy threat of predation. Moreover, personal odors of the birds themselves contribute profoundly to the olfactory signature of the burrow,

suggesting that individual or sex-based odors may play a role in nest relocation (Bonadonna & Nevitt 2004).

The pioneering studies exploring the idea that petrels use olfactory cues for homing were performed over 30 years ago on storm petrels, yet these ideas have only recently been seriously revisited in other species (Bonadonna et al. 2001, 2003d, 2004, Bonadonna & Nevitt 2004). Grubb (1973, 1974) found that Leach's storm-petrels *Oceanodroma leucorhoa* consistently approached burrows from downwind, suggesting that olfactory cues guided this behavior. He concluded that petrels could smell an odor plume emanating from the substrate near their burrow and use it to recognize and locate their own burrow's entrance. This idea was supported in subsequent experiments testing birds in Y-maze situations: Leach's storm-petrels tended to choose arms containing nesting material over arms containing forest-floor substrate.

More recent experiments have tested whether experimentally-induced anosmia (via obstructing the nostrils, transection of the olfactory nerve or chemical ablation of the olfactory epithelium) impairs homing (e.g. Benvenuti et al. 1993, Minguez 1997, Bonadonna & Bretagnolle 2002). Results from such studies suggest that a functional sense of smell is required to relocate the nest, at least for burrow-nesting species. Tests of other procellariiform species have produced inconsistent results suggesting that some species do not need olfaction to relocate their nest sites, whereas others do, depending upon the circumstances. Further, at least one preliminary study suggests that this behavior is flexible: in the case of Cory's shearwaters, the nocturnal subspecies *Calonectris diomedea diomedea* relies mainly on olfactory cues, whereas the diurnal *C. diomedea borealis* probably relies more on visual cues (reviewed by Warham 1996).

A recent comparative study conducted across different species suggests that, as with foraging, there is a relationship between life history and whether or not species use olfaction to relocate their nest site. Bonadonna & Bretagnolle (2002) have found that only birds nesting in burrows and returning to the nest at night require an intact sense of smell to relocate their burrows, whereas birds nesting on the ground or returning in the daylight can accurately locate their home even if they are anosmic. In subsequent Y-maze experiments, several species of burrowing petrels (blue petrels, thin-billed prion, and Antarctic prions *Pachiptila desolata*) required olfaction to recognize their home burrow (Bonadonna et al. 2003b,c, 2004). These results parallel our foraging model in that: (1) birds that nest on the ground use a combination of cues (visual, acoustic, and perhaps olfactory) to locate the nest site, whereas (2) birds that nest in burrows and return to the colony at night require olfaction to relocate the burrow.

Given that burrows have an olfactory signature recognizable to the individuals that occupy them, might the olfactory world of petrels be even more complex than we previously imagined? We are currently exploring this possibility. For example, we know that common diving petrels *Pelecanoides urinatrix* and South-Georgian diving petrels *Pelecanoides georgicus* are not attracted to food-related odors at sea and have the smallest olfactory bulbs among petrels (reviewed by Warham 1996). Yet these birds use olfaction to locate their burrows (Bonadonna et al. 2003d). The strong musky odor emanating from these birds suggests an individual component in the odor signature of the burrow, and we assume that this signature is a mixture of personal odor and the odor of the partner. Our current studies are exploring whether individual-specific odor cues are used in individual recognition among mates and conspecific neighbors (Bonadonna & Nevitt 2004). Among mammals, rodents use chemical communication in their social life, marking their breeding place and discriminating between kin and non-kin (Mateo & Johnson 2000). Given that many procellariiform species are philopatric to remote islands, where they are active on land, exploration of the use of scent in kin recognition, mate choice and possibly in inbreeding avoidance offer exciting topics for further investigation into the sensory ecology of these extraordinary birds.

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Role of the magnetic sense in the distribution and abundance of marine animals

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The ability to navigate accurately over long distances during homing and migration enables animals to exploit predictable spatial and temporal variations of the physical environment and corresponding variations in the availability of food. Accurate navigation in marine environments is not, however, easily achieved. Birds, fishes, whales, turtles and lobsters that migrate (or home) over distances of 10s to 1000s of kilometers encounter few landmarks in marine environments, may travel continuously for extended periods, and fre-

quently return to miniscule targets among the vast expanses of the oceans. Swimming and flying animals must also overcome passive displacement during movement through environments (water and air) that may themselves be moving with, against, or across the directions of travel. For example, the bar-tailed godwit *Limosa lapponica* flies non-stop for over 10 000 km across several easterly and westerly wind belts in the Pacific Ocean to New Zealand (Gill et al. 2005), which presents a target that is 2 to 3° wide when the birds set off on their migration. Such journeys must generate strong selective pressure for the ability to navigate accurately, particularly when travelling over long distances.

The magnetic field of the Earth has long been considered an environmental cue that could be used to guide travel over great distances, but the difficulty of demonstrating the existence of a magnetic sense has fuelled skepticism about the magnetic field's use (e.g. Griffin 1982). This skepticism has been heightened by the difficulty of obtaining robust experimental evidence that animals use the Earth's magnetic field in long-distance navigation (e.g. Wallraff 1999). Although a coherent picture of the structure and function of the magnetic sense is now being developed, much work will be required before we understand how animals use their magnetic sense. In seeking to identify how the operation and use of the magnetic sense influences the ecology of marine animals, we need to consider briefly both the Earth's magnetic field as a stimulus and what is known about detection of magnetic fields by animals.

The Earth's magnetic field. Besides providing the information about direction with which we are all familiar, the Earth's magnetic field provides 2 potential sources of information about location (the reader is referred to a detailed review by Skiles 1985, on which this section is based). These are: (1) systematic variation in the intensity (or strength) and direction of the field that might be translated by an animal's magnetoreceptor system into information for navigation over very large areas (Fig. 4A); and (2) localised variation in intensity due to magnetic rocks in the Earth's crust that might be used as magnetic landmarks or to identify specific locations such as seamounts.

At any point on the Earth's surface, the observed magnetic field can be described as a vector in 3-dimensional space (Fig. 4B). The total field vector (TFV) is the sum of fields arising from 2 main sources. The primary source is the field produced in the core of the Earth; this is the main field, which contains both dipole and non-dipole components that can be represented by a mathematical model (Skiles 1985). The dipole in the core dominates (generally >90%) the observed field and causes the magnitude (intensity) and direction of

the vector to vary systematically between the magnetic equator and the poles. The intensity of the main field varies between 25 000 and 65 000 to 70 000 nanoTesla (nT), or 2 to 5 nT km⁻¹, between the magnetic equator and poles. Similarly, the inclination of the Earth's magnetic field (the angle between the vector direction and the horizontal component of the field; Fig. 4B) varies from parallel to perpendicular to the Earth's surface between the magnetic equator and poles. Finally, the declination of the Earth's magnetic field is the angle between the directions of geographic and magnetic north and arises from the displacement of the magnetic poles relative to the geographic poles (Fig. 4B).

The second source of the Earth's magnetic field is the residual field (the field remaining after the main field has been subtracted from the observed TFV; Fig. 4C). The residual field is produced by the presence of magnetic minerals in the crust of the Earth. Concentrated deposits of iron ore, iron oxides and basaltic lavas produce fields that can be large enough to be considered magnetic anomalies. Although the residual field is generally << 5% of the total field, it varies much more rapidly and irregularly than the main field. Thus, intensity variations within magnetic anomalies may range from 10s to 100s (or even 1000s) of nT km⁻¹ over distances of from 100s of m to a few 10s of km.

Of particular interest in the marine environment is the new seafloor produced at mid-ocean spreading ridges. This seafloor occurs in distinct bands of positively and negatively magnetized rock (positive and negative magnetic anomalies) that are symmetrically arranged on opposite sides of the mid-ocean ridges. The process of seafloor spreading in the deep ocean results in linear magnetic anomalies (magnetic lineations) that are symmetrically arranged on opposite sides of the ridges (Vine 1966). A second pattern of magnetic anomalies, aligned at nearly right angles to the axes of the magnetic lineations, is produced by magnetization during the cooling of magma produced at fracture zones across the spreading ridges. These intersecting anomaly patterns are distributed over the whole of the deep ocean, are stable over very long periods, and remain present during reversals of the dipole field (Walker et al. 2002).

Thus, both the main and residual fields provide potentially useful information about location, but they operate over very different spatial scales and vary at rather different rates. The power spectrum for the Earth's magnetic field is bimodal with a minimum at wavelengths between 350 and 3500 km (Allredge et al. 1963). Wavelengths below 80 km are due to magnetic anomalies in the Earth's crust, whereas the wavelengths of the main field are generally >> 3500 km. When it is mapped, the residual field can be represented as a surface much like physical topography.

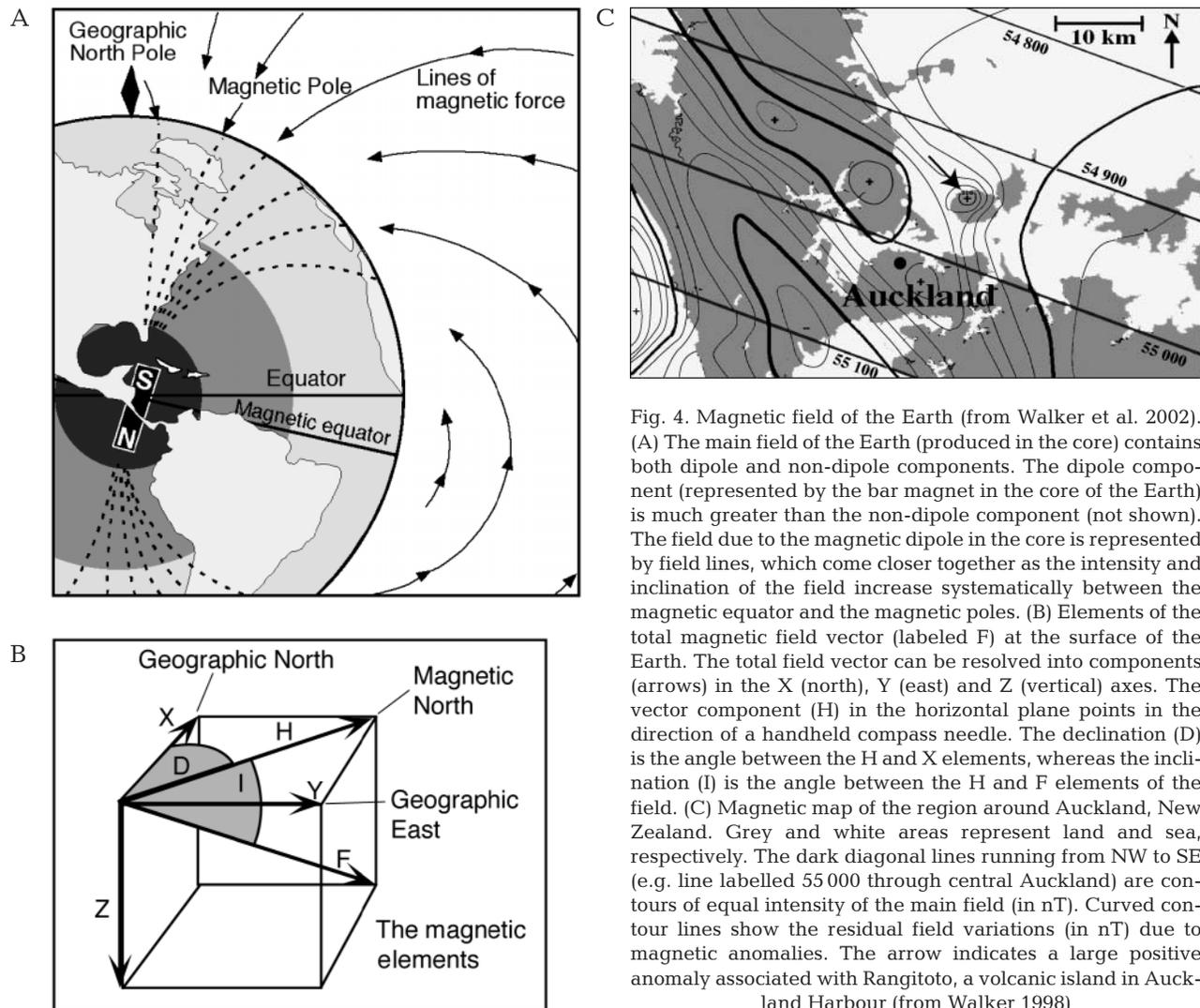


Fig. 4. Magnetic field of the Earth (from Walker et al. 2002). (A) The main field of the Earth (produced in the core) contains both dipole and non-dipole components. The dipole component (represented by the bar magnet in the core of the Earth) is much greater than the non-dipole component (not shown). The field due to the magnetic dipole in the core is represented by field lines, which come closer together as the intensity and inclination of the field increase systematically between the magnetic equator and the magnetic poles. (B) Elements of the total magnetic field vector (labeled F) at the surface of the Earth. The total field vector can be resolved into components (arrows) in the X (north), Y (east) and Z (vertical) axes. The vector component (H) in the horizontal plane points in the direction of a handheld compass needle. The declination (D) is the angle between the H and X elements, whereas the inclination (I) is the angle between the H and F elements of the field. (C) Magnetic map of the region around Auckland, New Zealand. Grey and white areas represent land and sea, respectively. The dark diagonal lines running from NW to SE (e.g. line labelled 55 000 through central Auckland) are contours of equal intensity of the main field (in nT). Curved contour lines show the residual field variations (in nT) due to magnetic anomalies. The arrow indicates a large positive anomaly associated with Rangitoto, a volcanic island in Auckland Harbour (from Walker 1998)

This suggests that the residual field could be used in much the same way as the visual landmarks in a physical topography can be used to navigate in a familiar area. This is especially true for the deep ocean where the magnetic lineations create a checkerboard pattern in the magnetic environment (Walker et al. 2002).

In contrast, the signal from the systematic variation (2 to 5 nT km^{-1}) at the scale of a travelling animal is very small compared with the residual variation (10s to 100s of nT km^{-1}) in the Earth's magnetic field. For example, it may take a 20 m long whale 5 min to swim 1 km (50 body lengths), during which time the main field may change by only 1 nT, unless the whale swims directly along the slope of the main field. Over the same time and distance, the animal may well experience a 10 to 50 fold greater change in the intensity of the residual field. This change in the intensity of the residual field will still be far less than a 1% change in

the total field, which is a relatively weak magnetic field (Skiles 1985). Thus marine animals will need to be able to detect extremely small changes in magnetic fields, whether they use the main field, the residual field, or both to navigate over long distances.

The magnetic sense. Critical evidence that some marine animals have a magnetic sense comes from conditioning and orientation experiments performed in the laboratory. Both teleost and elasmobranch fishes have been trained to discriminate magnetic fields in conditioning experiments (Kalmijn 1981, Walker et al. 1997). Similarly, teleost fishes, spiny lobsters, and sea turtles respond to either magnetic field direction or intensity when placed in orientation arenas (Quinn 1980, Lohmann et al. 1995, Lohmann & Lohmann 1996).

How animals may detect magnetic fields is being debated (see review by Lohmann & Johnsen 2000). Currently, discussion focuses on 3 main principles –

magnetic field detection based on magnetite particles, photopigments, and electrical induction. Single-domain magnetite suitable for use in magnetic field detection has been discovered in the heads of both fishes and birds (Walcott et al. 1979, Diebel et al. 2000). Perception of magnetic fields using photopigments, first suggested by Leask (1977), is thought to work by transduction of magnetic information when the ground states of visual photopigments are elevated to specific excited states by the ambient magnetic field. The theory of magnetoreception by induction is based on Faraday's law and assumes that magnetic information is perceived by electroreceptors such as the ampullae of Lorenzini of the elasmobranchs (Kalmijn 1981). Of these 3 mechanisms, only magnetite-based magnetoreception is thought to provide animals with the sensitivity necessary to enable position determination using the Earth's magnetic field (Walker et al. 2002). In no case, however, is it unequivocally established that one or other of these proposed mechanisms is indeed used to detect the Earth's magnetic field.

The magnetic sense in navigation. In order to navigate accurately between widely separated resources in the marine environment, animals must be able to determine their current location relative to some geographic target and then to set a course towards it (Kramer 1953). The magnetic and celestial compasses that animals use to set courses are relatively well understood, but the mechanisms used to determine position in the marine environment are unknown.

Determining position using the systematic variation of the main magnetic field requires that animals extract magnetic analogues of geographic latitude and longitude from the very small variations in the main field, and in the presence of the very much larger variations from the residual field. Although 2 models for obtaining magnetic analogues of geographic latitude and longitude from the systematic variations in the main field have been proposed (Lohmann & Lohmann 1996, Walker 1998), a mechanism for distinguishing the very small signal associated with the systematic variation in the main field from the noise due to residual fields has not yet been identified. Such a mechanism will almost certainly include filtering at the sensory receptor, processing, and behavioural levels of position determination.

If animals are able to screen out noise due to residual fields effectively, they should be able to use the Earth's main field to travel direct routes between locations, even over very large distances and after experimental or passive displacement. Seabirds foraging over the Southern Ocean are able to fly relatively direct routes home, both after foraging journeys up to 2000 km from home over several weeks, and after experimental displacements of several 100 km (Benhamou et al. 2003).

Circumstantial evidence that residual fields may interfere with use of the main field in navigation comes from the observation that fin whales migrating along the eastern seaboard of the United States avoid areas of high magnetic intensity and gradients associated with strong residual fields (Walker et al. 1992).

The disadvantage of using the main field of the Earth for navigation is that there may be some limit to the ability to filter out the noise from residual fields. The accuracy of the initial orientation of homing pigeons is affected by the intensity of magnetic anomalies and magnetic storms (Keeton et al. 1974, Walcott 1977). These observations are consistent with studies reporting the locations where deep-water odontocetes (such as pilot whales) strand themselves alive. Such strandings often occur at areas where there are strong residual fields (Kirschvink et al. 1986). However, not all whales that enter shallow water appear susceptible to the effects of residual fields. During summer, fin whales feed in the Gulf of Maine and around the New England seamounts (Walker et al. 1992), but do not live-strand, perhaps because they become familiar with the types of residual fields experienced in shallow water at both their summer feeding and winter breeding sites.

In contrast with the main field, use of residual fields for navigation requires only that the magnetic sense be able to detect small changes in the total intensity of the Earth's magnetic field. Residual fields are not regularly distributed in space outside the deep ocean, so the pattern of magnetic field changes experienced will be highly dependent upon the direction in which the animal travels through the residual fields in any geographic region. Use of residual fields for navigation outside the deep ocean (e.g. continental shelves) will, therefore, require recognition of individual magnetic anomalies, and this requires familiarity with the magnetic landscape. For example, scalloped hammerhead sharks make regular foraging journeys over distances of up to 20 km between the Espiritu Santo seamount and Las Animas Island in Baja California, apparently following particular magnetic features that are independent of bathymetry (Klimley 1993).

The magnetic lineations in the deep ocean are clear patterns in residual field variation that animals could use to navigate (Kirschvink et al. 1986). If animals navigate using magnetic lineations, it can be predicted that they will preferentially follow features that are consistent with their migration direction. Furthermore, animals on their first migration will need to travel with individuals that know the route from previous journeys. Magnetic anomalies, therefore, will most likely be used by animals that either: (1) travel long distances in groups with animals that have previously travelled the route, using magnetic lineations as landmarks; or

(2) remain within a familiar area and normally only travel distances of up to some 10s of km. In the first case, strong social ties, as in some mysticete whales, are likely to be a precondition for long-distance migration (because routes are learned). It will be important to establish from tracking studies how dependent successful migration is on such social groups, as disruption of social structure may result in loss of the migratory behaviour in some populations.

Ecological and evolutionary implications of magnetic navigation. For animals that use the Earth's main magnetic field to navigate over large distances, homing and migration permit access to the energy flux from the Sun over huge areas. In the absence of other influences, the increase in food resources resulting from the ability to navigate over long distances should facilitate population growth and the establishment of larger species distributions. Higher abundances and wider distributions should commonly result in larger and more diverse gene pools (because of increases in the number of successful mutations and local adaptations to environmental conditions; Wirth & Bernatchez 2001). Large gene pools have 2 potential consequences that depend on demographic properties: (1) They should promote local adaptation and diversification of species when isolated, discrete, habitats are colonised (merely by increasing the probability of successful colonisation of such habitats). (2) Populations with larger gene pools should resist genetic change under conditions of mixing in continuous environments. Thus, within an ocean basins genetic heterogeneity in cosmopolitan marine fishes is lower in continuously distributed species and higher in discontinuously distributed species (Graves 1998).

Migratory species will be better able than sedentary species to avoid local extinction through catastrophic environmental change (e.g. volcanic eruptions). Similarly, the distributions of migratory species may contract during ice ages, but can expand rapidly as the climate warms again (Alerstam 1990). In contrast, sedentary species may well be driven extinct by glaciations, or else be marginalised into relict populations from which their distributions cannot expand again after the ice retreats. Sedentary species are also far less likely to encounter opportunities for colonisation of novel environments (such as newly formed volcanic islands) located far from other landmasses.

Navigation using the residual magnetic field. The spatial extent of navigation using residual fields should largely be restricted to distances of <80 km. This is because the wavelengths of such fields are most pronounced at this and lesser distances over the Earth's surface. Areas of low residual fields are also likely between major magnetic features (such as many seamounts). As a consequence, species that navigate

using residual-field features only may well have limited dispersal abilities, which may contribute to higher rates of speciation within limited distributions. A possible exception to this pattern is the use of residual fields as 'leading lines' to guide migration in the deep ocean. For instance, Kirschvink et al. (1986) proposed that the magnetic lineations could be used to guide migration over the deep ocean. This hypothesis predicts that the paths travelled by migrating animals should follow magnetic lineations for substantial distances. A possible example of the use of magnetic lineations as a 'leading line' during migration is the observation that <1% of albacore tuna tagged on either side of the Mendocino Fracture off Cape Mendocino (near San Francisco) crossed the fracture within the year in which they were tagged (Lauris 1979). Up to 5% of the fish were, however, found on the opposite side of the fracture after they had completed their return migration across the Pacific to Japan; that is, after the fish had had a chance to swim around the end of the fracture, NW of Hawai'i.

Where to from here? One unique property of the Earth's magnetic field is that it provides consistent information that is available throughout the biosphere and that can be used for navigation over distances ranging from a few to many 1000s of km. The properties of the main and residual magnetic fields, together with the known properties of the magnetic sense, suggest 2 main strategies for navigation using the Earth's magnetic field. (1) We propose that navigation using the main field permits the large-scale distributions and contributes to the high abundances of some migratory species through the access it provides to primary productivity over very large areas. Depending upon specific life-history patterns and environmental conditions, this strategy will permit resilience against both local catastrophic and large-scale environmental changes, as well as speciation through adaptation to local conditions. (2) Conversely, we suggest that use of the residual field for navigation will be associated with restricted distributions, limited dispersal ability, philopatry and localised speciation. If these navigation strategies are indeed used by animals, psychophysical studies of their magnetic sense should reveal differences in the responses to systematic variations in frequency and intensity of experimental magnetic fields among species using the different strategies.

We would also expect to see bimodality in the magnitude of typical travel distances and in the behavioural responses to experimental displacement by the species that use these navigational strategies. In particular, we anticipate that animals that use the main field will travel long distances by relatively direct routes and be able to return to defined locations after

displacement, whereas animals that use residual fields would travel shorter distances and will tend to follow recognisable features in the residual field, particularly after displacement.

The widespread availability and utility of devices permitting the accurate determination of location (such as GPS) facilitates studies of the manner in which animals use of the Earth's magnetic field to navigate. With this, and similar technological developments, we can look forward to many exciting discoveries in the years to come.

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