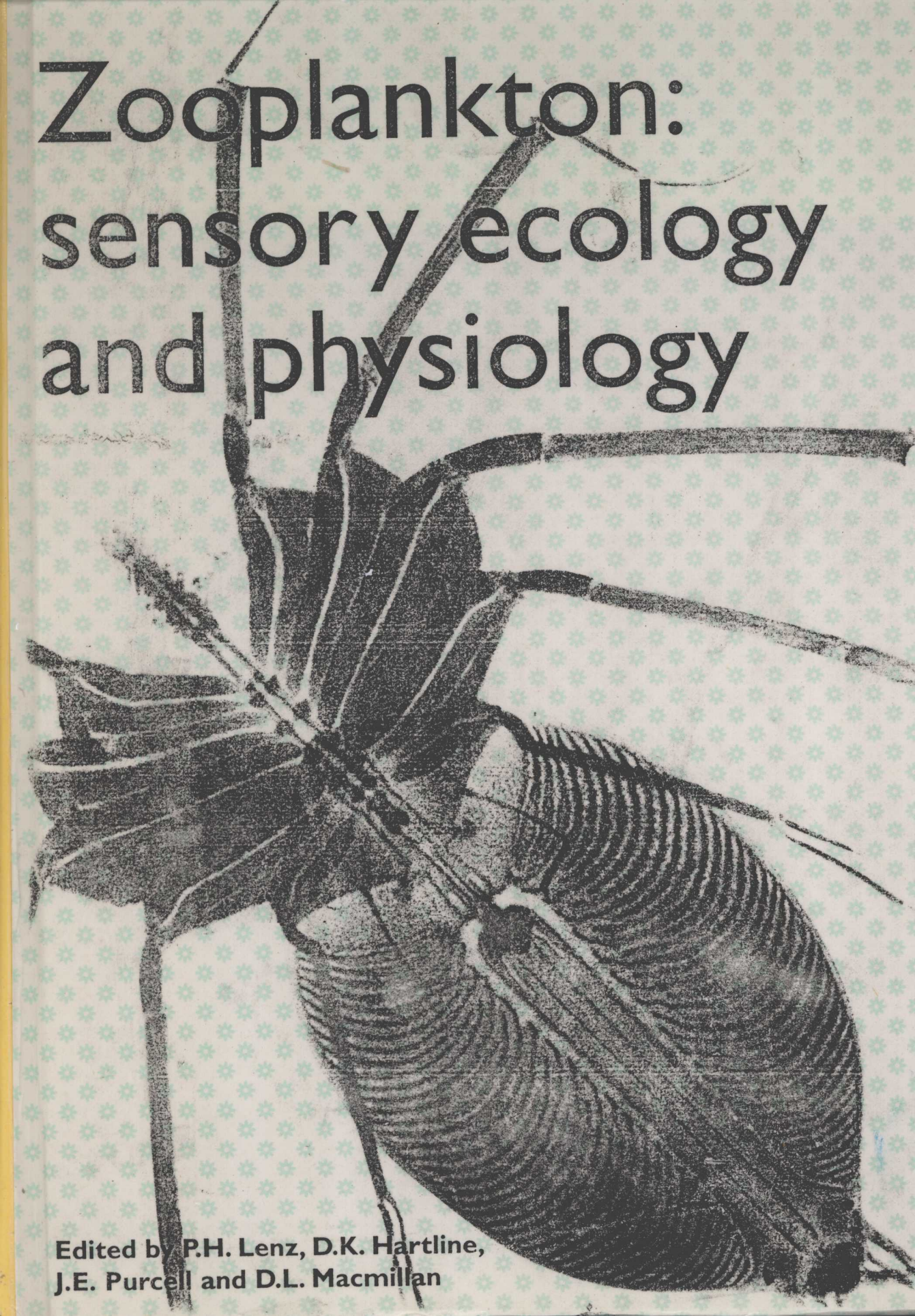


Zooplankton: sensory ecology and physiology



Edited by P.H. Lenz, D.K. Hartline,
J.E. Purcell and D.L. Macmillan

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Detail of Planktonic Phyllosoma Larva (stage X) of the Rock Lobster

Jasus edwardsii

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Introduction

Planktonic organisms constitute a major portion of the planet's biomass, biodiversity and food base. Traditionally the fields of biological oceanography and limnology have been concerned with planktonic production and the transfer of energy from one trophic level to another, where the focus is on the group rather than the individual. As the quantitative relations among different parts of pelagic food webs are determined with increasing precision, difficulties in accounting for observed interactions make it clear that more detailed information is needed about particular species and the interactions among members of plankton communities.

Sensory systems provide animals with information about their environment that is necessary for them to survive and reproduce, and hence maintain their position in the community. Oceanographers and limnologists have long been aware of the special sensory challenges facing animals with a planktonic lifestyle. Complex interactions between them, extensive migrations and orientation in water masses and currents are just some of the behaviours of zooplankton that have intrigued researchers. Because they are generally small and fragile, few physiological studies have been made on zooplankton but those few suggest that sensory systems among planktonic organisms differ in many significant ways from those of benthic forms.

A substantial body of information has accumulated over the past two decades on the behaviour of zooplankton in both field and laboratory. The interpretation of these behavioural studies has been hampered, however, by a limited knowledge of the underlying sensory mechanisms. The frustration this has generated in the scientific community is apparent from the repeated calls for additional information on sensory systems in planktonic organisms (e.g. Marine Zooplankton Colloquium I., "Future marine zooplankton research – a perspective", *Mar. Ecol. Progr. Ser.* 55: 197-206, 1989). The focus of sensory neurobiologists, however, has generally been on particular physiological processes, which are studied in accessible animals that

serve as convenient models, adult benthic molluscs and crustaceans and adult fishes, for example.

Recent technological advances have opened the way for the application of neurobiological techniques to small planktonic organisms. Concurrently, new designs in video recording and analysis have expanded behavioural studies in both the laboratory and field. Unfortunately, neuroscientists, marine biologists, biological oceanographers and limnologists do not often attend the same scientific meetings nor do they publish in the same journals. An improved flow of information among these disciplines is likely to elucidate many important aspects of the sensory biology of zooplankton, ranging from morphology and physiology to ecology and evolution.

In order to encourage interdisciplinary investigations of these aspects of biological processes in the marine pelagic environment, we convened a diverse group of scientists in Honolulu in January, 1995. Many of the presentations at the meeting were subsequently prepared for publication. All submitted papers were subjected to full peer review*.

Rather than the more traditional grouping of sensory studies according to sensory modality, we have used taxonomic groupings which bring into proximity papers concerned with a particular group's role in the community structure and thereby emphasize the fact that several sensory modalities must work in concert to permit organisms to survive in their ecological niches. The broad neurobiological principles which serve as a starting point for an understanding of zooplankton sensory systems at the cellular level are laid out in several papers on non-planktonic organisms.

*All chapters in this volume were accepted following the full peer review procedure of the Journal *Marine and Freshwater Behaviour and Physiology*, in which versions of some of these and other contributions were published.

Comparisons of sensory inputs to pelagic and benthic organisms are highlighted in papers on sensory characteristics and by experimental approaches used in well-studied vertebrate and invertebrate models. Hopefully, this will encourage the application of similar approaches to zooplankton in the future.

In the absence of direct studies on zooplankton, such examples may give us the best direction on how to approach further studies on zooplankton. The contributed papers give details of a diversity of behavioural adaptations that are critically dependent on sensory mechanisms, as well as information on some of the underlying structures and mechanisms.

The challenge to all of us interested in zooplankton sensory systems is to combine what is known and what is continuing to be discovered about zooplankton behaviour and ecology with information derived from neurobiological approaches, to better understand the sensory world of small pelagic animals. As emphasized by Ted Bullock in his plenary paper, there are many unexplored leads and opportunities that point to the way neuroethological approaches can contribute to our understanding of zooplankton behaviour.

On a trial basis, for a indeterminant time, we will maintain a site on the World Wide Web dedicated to disseminating information on zooplankton sensory systems:

<http://www.pbrc.hawaii.edu/~lucifer>

We welcome contributions and comments.

*Petra Lenz
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NEUROETHOLOGY OF ZOOPLANKTON

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Application of a neurophysiologist's techniques to the study of zooplankton sensory systems need not be ruled out on the basis of small size or slipperiness. Successes in this endeavor are accumulating steadily. Zooplankton offer a rich source of opportunities for interesting and different sensory systems for neuroethological investigation. Behavioral studies already suggest a number of fruitful areas for sensory physiological investigation. In other cases, sensory structures have been found which invite both physiological and behavioral study. Sensory capabilities found in non-planktonic groups are likely to appear also in planktonic forms, but with their own unique characteristics reflecting the planktonic life style. Following the main discussion is a bibliography of recent papers, and a selection of earlier ones, related to the themes discussed.

INTRODUCTION

Whereas the neural analysis of behavior of planktonic species and stages has been relatively neglected, we have many clues that it is going to be rich, diverse and interesting. The aims of this contribution are to defend that statement, with selected examples, and to suggest that neural analysis, particularly sensory physiology, has great explanatory power of ecologically significant behavior.

I have to begin with a personal note about plankton, recalling the lasting impression made long ago by a film on invertebrates in the Arctic where scyphomedusan jellyfish were pulsing at a rate well within the range familiar in summer temperate waters, warmer by 20°C. I must have been influenced by this observation and my own experiences in a study of the neural basis of fluctuations in the rate of pulsation of medusae (Bullock 1943), some of which was made in December 1941 in Pensacola, where my wife and I collected *Rhopilema* cruising at random in the Sound, stopped now and then by Army bridge guards concerned about saboteurs in that first fortnight after Pearl Harbor. At any rate, by the early fifties about half of my laboratory group was devoted to the physiological ecology of temperature acclimation in marine invertebrates. That field, which I left in the early sixties, still offers a challenge in the ecologically fundamental question of why some species are able to acclimate much more than others. The proposal I made in 1955, that different rates in the same organism acclimate to different degrees, resulting in greater disharmony in some species than others, may still be viable and most likely applies to rate processes in sensory and central nervous functions, among others.

Medusae are large animals, relatively, although generally treated as planktonic. The first reaction from most workers when neurophysiology of plankton is mentioned concerns their small size or gelatinous nature. The first message I bring is not new but also not widely appreciated.

SMALL SIZE AND SLIPPERINESS ARE NO EXCUSE

Techniques have been successfully developed to record nerve impulses from single neurons in zebra fish larvae (Eaton and Kimmel, 1980). (*Only one or a few sample citations are given, here and in the following, often representing a substantial literature*). Many papers deal with electrical recording from small flies (Ogmen and Garnier, 1994), even *Drosophila* (Wyman *et al.*, 1984; Elkins and Ganetsky, 1990; Engel and Wu, 1992; Trimarchi and Schneiderman, 1993) and mosquitoes, and from copepods (Yen *et al.*, 1992). Single unit action potentials have been recorded from scyphomedusans (Horridge 1953), *Clione* (Arshavsky *et al.*, 1988, 1991, 1992; Huang and Satterlie, 1990; Satterlie, 1993; Norekian, 1989, 1993; Norekian and Satterlie, 1993b), *Melibe* (Trimarchi and Watson, 1992), a number of other opisthobranchs, and cephalopods (Maturana and Sperling, 1963; Laverack, 1980; Boyle *et al.*, 1983; Bullock and Budelmann, 1991) and larval fish (Eaton and Nissanov, 1985 mentions a predatory protozoan causing escape responses in larval zebrafish; Eaton and DiDomenico, 1986). Many studies have been done upon unanesthetized animals, free to move and behave, within limits.

BEHAVIOR TURNS UP NEW SENSES AND FORMS OF RECOGNITION TO BE ACCOUNTED FOR

The chief source of clues to sensory biology and interesting neuroethology of zooplankters is the close observation of their behavior and responses. I will cite some examples that present opportunities for new analysis of their neural bases.

Responses to pure hydrostatic pressure stimuli have been reported in a number of species (Morgan, 1984; Forward, this symposium). Following earlier suggestions from much greater stimulus intensities, Knight-Jones and Qasim (1955) Baylor and Smith (1957) and Enright (1961, 1962, 1963, 1967) found responses to changes in pressure as low as 10 cm of water or 10 millibars (mb). Knight-Jones and Qasim provided no details about their experimental methods but reported up-swimming to increases and down-swimming to decreases of 10 mb in *Carcinides* and *Galathea* megalops larvae. Baylor and Smith found lower thresholds in pteropods and copepods (*Pontella*, *Temora*) and, like the previous authors, thresholds of < 1 atmosphere in annelids, hydromedusae, chaetognaths, ctenophores, copepods and others. According to my memory of their verbal presentation, though not in the brief printed version, Baylor and Smith, in one type of experiment, watched individual zooplankters in a vertical glass cylinder, swimming up and down within a range of a few centimeters. They then raised or lowered a leveling bulb connected to the cylinder – whose top was closed – by a flexible U-tube, following each vertical movement of the animal. Keeping the pressure constant at the level of the animal, it increased its vertical excursion markedly, as though lacking the normal change-of-pressure feedback. This behavior implies a non-drifting, absolute pressure sense. Baylor and Smith report that a 15 cm stimulus causes a 15 cm response in the compensatory direction. They emphasized that reliable responses require animals brought in with extreme care to avoid pressure or pH or other shocks. Depth compensating responses by planktonic animals had been reported in some species to persist with undiminished intensity for several hours (Hardy and Bainbridge, 1951, who used stimuli in the 500 mb range), and have therefore been interpreted as

indicating a sort of "barostat" by which the animals might maintain constant depth, to within a few meters in the sea.

In contrast to the sustained type of response, which requires a tonic receptor, Enright observed transient but intense behavioral responses in *Synchelidium* sp., an intertidal, predominantly benthic amphipod. He did not exclude their having some sustained sense but showed the importance of the phasic component. He started with many amphipods in a closed jar of sea water, most of them resting on the bottom. Raising the leveling bulb or adding small weights to a piston, both of which were done in the next room, in double blind experiments, caused many animals to swim about vigorously for a few seconds. Decreasing the pressure caused transient reduction of ongoing spontaneous activity. He later found similar responses in the anomuran *Emerita*, particularly the megalops larval stages, immediately after they have settled following a prolonged planktonic development. He excluded the possibility of small gas bubbles, and we have no precedent for other structures with appreciable compressibility different from aqueous tissues or with piezoelectric properties immersed in aqueous tissues. Digby (1961) proposed a mechanism involving a monolayer of gas but his evidence has not been generally accepted. Even in the best studied species, *Emerita*, we do not know where the reception occurs. Enright has observed responses in some individuals after removal of all pereopods or all four antennae or both eyes (pers. comm.). I believe a hitherto unknown sense organ, indeed a new class of sense organs is awaiting discovery. Only after localizing and identifying the organ can we expect to deduce the detection principle it employs.

Mechanoreceptors for water movement and vibration are probably among the most amenable to new physiological study (Newbury, 1972 in chaetognaths; Wiese and Marschall, 1990 in euphausiids). Lateral line-like sense organs have been reported in penaeid shrimps (Denton and Gray, 1985) and in cuttlefish (Budelmann this volume; Budelmann and Bleckmann, 1988; Budelmann, 1989; Budelmann *et al.*, 1991; Bleckmann *et al.*, 1991a; Bleckmann, 1994).

Also awaiting discovery in zooplankton are temperature receptors, especially those with a non-adapting, thermometer-like response that can explain the known behavioral response manifested by a consistent thermopreferendum. It has been repeatedly pointed out that at least teleosts and probably many taxa and stages of development show an ability to stay in a layer of water of a preferred temperature, to within a fraction of a degree, i.e. to close to an isotherm. It seems unlikely that this is explainable in the general case by a parallel isodensity (Forward, 1989b and this symposium) or other clue. If it is, then yet another non-adapting sensory receptor is to be sought. Thermometer organs are well known in mammals, including those that are excited by increases in temperature in the normal living range ("warm receptors") and those that are excited by decreases in temperature in this range ("cold receptors"). They are believed to occur in fish and other exothermic taxa but a convincing demonstration of specific temperature sense organs is an outstanding opportunity (Späth, 1978), particularly in zooplankters. The adapting aspect of sense organ response, i.e. a temperature rate-of-change sensibility is likely to be found first, either in separate receptors or as an initial part of the response of thermometer-like receptors (Forward, 1990b, and this symposium). But, the experience with the ampullae of Lorenzini of elasmobranchs warns us to be cautious; they were first thought to be very sensitive temperature change receptors (Sand, 1938) and only later was this modality shown not to be the normal adequate stimulus (Bullock, 1974).

Chemoreceptors are indicated by many behavioral observations which, moreover, point to high specificity and sensitivity (Lazzaretto *et al.*, 1990; DeMott and Watson, 1991; Kassimon and Hufnagel, 1992; Snell and Morris, 1993; Bollens *et al.*, 1994, to cite only some of the more recent reports).

Some kinds of behavior have yet to be found, but I believe, will be found in zooplankters and will then trigger the search for the organs mediating them. An example is magnetic orientation, known in bacteria (Kalmijn, 1978; Blakemore *et al.*, 1980), where the behavior is apparently adequately accounted for by a known organelle. The behavior has often been claimed for birds and insects but no sense organ or identified transducer has been convincingly shown as yet. Lohmann *et al.*, (1991) report a particular pair of cells in the gastropod, *Tritonia*, that alter their firing in response to changes in earth-strength magnetic fields; the same field changes do not influence any of 50 other cells.

Magnetic orientation as an indirect consequence of highly sensitive electrosensory organs and central pathways and processors able to extract this information and use it in normal behavior, has been shown in elasmobranchs (Kalmijn, 1988). A similar sense exists in some quite small teleosts, marine (*Plotosus*, *Arius*, Siluriformes), as well as freshwater (Siluriformes, Gymnotiformes, Mormyriiformes and one subfamily of Osteoglossiformes). At present, however, none but the elasmobranchs are known to have an adequately high sensitivity to make use of the currents induced by motion in the earth's magnetic field. Still, neither the sensitivity in these groups, already known to be electrosensitive, nor the existence of this sense in other taxa, both vertebrate and invertebrate, can be categorically ruled out. I anticipate new findings of both electrosense and direct magnetic sense.

Other forms of behavior are quite familiar and yet the sensory modalities involved are only partly or little known. Schooling in teleosts and other groups, including members of the zooplankton, seems likely to depend on more than one sense in different species and conditions (Partridge and Pitcher, 1980; Wiese, this symposium). I doubt that our present understanding, based on a few species, is a representative picture of this widespread class of behaviors. To mention one example, Kalmijn (personal communication) has suggested that the dense schools of the marine catfish, *Plotosus*, may under some conditions use their electrosense to keep together.

Other familiar behaviors whose sensory bases are rarely or little known are predator avoidance, prey detection, conspecific communication and mate recognition. Data on fish kairomones that influence the avoidance or swarming behavior of *Daphnia* are presented elsewhere in this symposium (Larsson; Ringelberg and van Gool; DeMeester). Finicky settlement of barnacle, polychaete and other larvae upon substrates according to its "taste" or texture is well known (Johnson and Strathmann, 1989; Harvey, 1993; Dineen and Hines, 1994; Forward, Zimmer-Faust, this symposium). Long ago I reviewed the literature on predator recognition by invertebrates and found few examples at that time, apart from scallops and freshwater snails (*Planorbis*); I reported observations of limpets and abalones fleeing from a starfish tubefoot (Bullock, 1953b). Specific chemical signals must be much more common than we then appreciated. The swimming escape response triggered by a brief contact with starfish tubefeet in the sea anemone, *Stomphia* (Wilson, 1959) and the nudibranch, *Tritonia*, (Willows and Hoyle, 1969) have been studied physiologically; in the latter case a network of neurons was identified that makes the decision whether to trigger the prolonged behavior.

Complex visual form recognition is indicated by behavior such as the use of dozens of distinct color patterns for as many social signals, shown by Moynihan and Rodaniche (1982) in a Caribbean squid (*Sepioteuthis*). Startle responses are a fertile field, convenient for sensory analysis because they are relatively stereotyped and hence successive experiments are likely to represent the same behavior. In the wide variety of taxa where they are found, different adequate stimuli are known, from a moving shadow to a tap or an acoustic click (Eaton, 1984). Mackie (1990) has pointed out interesting parallels between the giant fiber jet swimming in squid and jellyfish, a form of behavior that is not stereotyped but quite flexible (Otis and Gilly, 1990). Careful experimental ethology may reveal that in some cases several stimuli of different modalities may function in sequence to bring an animal into close proximity with a desirable target or prime it to be more sensitive to some forthcoming event.

A POINT OF VIEW MAKES YOU A NEUROETHOLOGIST

Ecologically significant behavior opens another dimension when we begin to uncover the mechanisms in sensory physiology, central analysis of sensory input, recognition of species characteristic sign stimuli, plastic modulation by age, state or other sensory inputs, selection of response from the species repertoire and neural control of effectors. With emphasis on the sensory side, I will illustrate with a selection of examples from near-planktonic or related or paradigmatic species that have received some successful study. These are intended to underline the opportunities and needs in further extension to the great range of planktonic taxa. It is important to note that, whereas some started with known behavior to be accounted for, others began as bottom-up or inside-to-outside or anatomy-to-physiology curiosity. Sometimes the relevant behavior has yet to be defined.

A good example is the discovery of a sensory system in cephalopods – actually in young, planktonic cuttlefish (*Sepia*), that appears to be an analogue of the lateral line system in aquatic vertebrates (Budelmann and Bleckmann, 1988; Budelmann, 1989; Budelmann *et al.*, 1991; Bleckmann *et al.*, 1991a; Bleckmann, 1994). Anatomical suggestions of possibly sensory structures are widespread (Hayashi and Yamane, 1994; Jensen *et al.*, 1994) and led the physiologists in this case to look for responses in the rows of cutaneous organs on the head. They proved to be responsive to disturbances in the water and not to other stimuli – a new modality for molluscs.

Quite a different story is represented by a recent finding in a classical sense organ in a squid (*Alloteuthis*), the statocyst. Here Williamson (1989) surprises us with the demonstration of electrical coupling between secondary hair (sense) cells – a step toward uncovering the cellular mechanisms of reception. Arkett and Mackie (1988) have shown the sensory hair cells for mechanoreception in the planktonic medusan, *Aequorea*, to be amenable to physiological study. The same must be true for water movement sensors in many other groups (Budelmann, 1989; Bleckmann, 1994). The sharp distinction found in vertebrates between the lateral line and the inner ear reception of disturbance in the aquatic medium outside the animal has yet to be properly compared with an adequate sampling of invertebrate systems. A large literature exists on the physiology and anatomy of hearing in fish (Atema *et al.*, 1988; Kalmijn, 1988; Popper, this symposium), including some small enough to be marginally planktonic and including very young sharks (Bullock and Corwin, 1979). A smaller but substantial literature exists on the lateral line (Coombs *et al.*, 1989). One

feature of the octavolateral sense organs of vertebrates which may have deep significance for their function in planktonic stages of fish is that the number of sensory hair cells increases with size dramatically. Presumably this confers greater ability to detect feeble signals and one has to wonder whether larvae and young fish are relatively deaf. Whereas well controlled behavioral experiments on adequately motivated animals are the final arbiter, simple electrophysiological endpoints may often be the first way to study such questions as the upper frequency limit of hearing or the influence upon hearing of the developing swim bladder and, in some species, its later disappearance. We found in young yellow-tail tuna (*Thunnus albacares*) that brain responses to inner ear reception cut off sharply above the remarkably low frequency of 350 Hz, even lower than an earlier report based on conditioned responses in two specimens (Iversen, 1967; Bullock, Brill and McClune, unpublished experiments).

Electroreception has already alluded to. Many species of agnathans, holocephalans, teleosts and others have been shown to be electroreceptive – more readily by physiological than by behavioral responses (Bullock *et al.*, 1961; Bullock and Heiligenberg, 1986; Fields *et al.*, 1993). Other taxa with this sense modality seem likely to be found, especially among teleosts, but small size confers a serious disadvantage. Sometimes the technic for recording from single receptors is exceedingly simple and requires no surgery (Viancour, 1979; DeWeile, 1983).

Photoreception and vision have attracted much attention among invertebrates (Therman 1940; MacNichol and Love, 1960a, b; Wiersma *et al.*, 1961; Waterman and Wiersma, 1963; Gwilliam, 1963; Hartline and Lange, 1974; Lange and Hartline, 1974; Lange *et al.*, 1974; York and Wiersma, 1975; Schiff 1987, 1989; Cronin *et al.*, 1994) including a few studies on planktonic forms (Smith and Macagno, 1990; Frank and Widder, this symposium). I expect many adaptive specializations to be found among zooplankters – for detecting color, moving shadows, dim light and the like.

What is taste and what is olfaction? Why are they so distinct in the peripheral and central structures that mediate them in the vertebrates – already in aquatic taxa, long before terrestrial forms evolved? These questions come primarily from the anatomy and physiology but depend on ethology and ecology for essential clues. Taxa differ greatly in the mechanisms of chemoreception and comparative physiology is essential, in parallel with comparative behavior, to understand the dynamic range, degree of specificity, temporal and spatial resolution of these senses.

I like to tell how important taste was in the history of the Scripps Institution of Oceanography and of the unique concentration of neuroscientists in La Jolla. Yngve Zotterman, Professor of Physiology at the Royal Veterinary College in Stockholm, was a prominent comparative physiologist of gustation. He started the series of international congresses on Olfaction and Taste, of which the volume edited by Kurihari, Suzuki and Ogawa (1994) is the eleventh. He visited his fellow Scandinavian, Per Scholander, in La Jolla, in 1959. Scholander was a comparative physiologist of respiration, cardiovascular, water and salt functions and got Zotterman to support his idea of a laboratory vessel dedicated to comparative physiology and biochemistry by showing how he would set up to record nerve impulses from taste fibers in teleosts on board one of the smaller Scripps vessels at sea. Yngve didn't succeed on that trip but supported Pete's idea, which led shortly to the R/V *Alpha Helix*. After that, one thing led to another until Pete and others at S.I.O. recruited the first neuroscientist to La Jolla, in 1965 – Susumu Hagiwara, who was followed by a swelling stream of like ilk, now many hundreds strong, more than a score of them doing marine biology. In spite of a substantial literature (represented in our reference list by Finger and

Silver, 1987; Atema, 1994; Atema and Voigt, 1995), the spectrum of taste receptors and even more of olfactory receptors is still only fragmentarily known, even in the most studied arthropods, molluscs and fish.

In order to do justice to the ecologically significant neuroethology of zooplankters, we have to look a bit farther along the central nervous pathways from sense organ to behavior. I will mention only a few examples from taxa that include planktonic members deserving study.

Giant fiber systems have been evolved again and again, convergently, among the phyla and classes; even orders and families may differ profoundly in the development of these systems (Bullock, 1948a, 1953a), usually associated with startle responses and the first phase of escape (Eaton, 1984). They are quite amenable to study in small forms, as already pointed out for *Drosophila* (Wyman *et al.*, 1984), even with extracorporeal, non-invasive electrodes (Featherstone and Drewes, 1991). The meaning of the giant fiber diameter cannot always be its greater velocity, for in small animals like *Drosophila* the absolute saving in time is small. Nevertheless, in some shrimp, adaptations of the giant fiber for high velocity result in phenomenally fast axons – by far the fastest known (Fan *et al.*, 1961; Huang and Yeh, 1963; Hsu *et al.*, 1964, 1975a, b; Hao and Hsu, 1965; Kusano, 1965, 1966, 1971; Hsu, 1982; Terakawa and Hsu, 1991). This is an elegant case where a simple property revealing a remarkable specialization was overlooked for decades, even though shrimp giant fibers had been studied and shown to be unusual (Holmes *et al.*, 1941).

Motor output, its patterning, and central and peripheral organization intimately complement the sensory input and are sure to be of interest in zooplankters. Some illustrative studies include that of Spencer (1988) showing non-spiking interneurons in the swimming system of a pteropod and of Arshavsky *et al.*, (1988) who found nonsynaptic interaction – both discoveries being of general neurobiological import. Arshavsky *et al.*, (1991, 1992) and Satterlie (1993) represent a series of studies of the organization of the swimming system in these gastropods. Wilson (1960) studied the nervous control of movement in annelids, and Bowerman and Larimer (1976) that in crustaceans. A number of chapters in Sandeman and Atwood (1982) and Wiese *et al.*, (1990) have relevant recent examples. Moss and Tamm (1993) show that even the delicate movements of ctenophores can be successfully studied with electrophysiological methods. Important effectors other than moving major parts of the body include the chromatophores. Some studies on them and their control underline the opportunities (Cooper *et al.*, 1990; Hanlon *et al.*, 1990; Novicki *et al.*, 1990), especially when cephalopods in good condition can be as readily available as they are now (Hanlon *et al.*, 1978, 1983). Nervous control of luminescence is also interesting and approachable (Nicol, 1960; Baxter and Pickens, 1964; Latz *et al.*, 1990; Bowlby and Case, 1991; Bannister, 1993).

ANATOMY HAS MANY NEW TOOLS AND RICH REWARDS

Although our symposium emphasizes sensory ecology and physiology, I must call attention to the opportunities for advancing both of them through anatomical investigation. The armamentarium of available new methods, especially those applicable to revealing neural organization has expanded dramatically in recent years and most of the newer procedures have yet to be exploited on zooplankters. Immunocytochemistry, intracellular dyes and markers transported throughout a

neuron and its processes, even in fixed material, laser confocal microscopy and the use of optical signals of activity, with or without voltage-sensitive dyes are some of the technics now in use for identifying and tracing nerve cells and their connections, distinguishing among types of neurons and visualizing active neurons. A limited selection of examples concern the retina (Saidel 1980; Saidel *et al.*, 1983; Cronin *et al.*, 1994; Arikawa and Matsushita 1994; Becerra *et al.*, 1994; Evans *et al.*, 1993; Munz and McFarland 1977). A selection on other sensory and central structures is represented by the reports of Tamm and Tamm 1991; Bollner *et al.*, Bundy and Paffenhöfer 1993. Many sense organs have been long known anatomically, or more recently recognized, but are still without any secure assignment of function. An example is the dorsal organ of many crustaceans, including planktonic taxa (Laverack and Sinclair, 1994).

THE CODA INTEGRATES THE THEMES AND LEITMOTIFS

Our organizers have rightly called attention to the great gap in understanding the principal fauna of the bulk of the biosphere. However complete our list of species, our zoogeography, foodwebs, and life histories, we cannot claim understanding before we know a good deal concerning what each zooplankter does about food, enemies, mates and other conspecifics, diurnal and seasonal states, what it can recognize and discriminate, what behavior follows each adequate stimulus, the pattern of succession of the behavioral repertoire – and the sensory and neural apparatus that accomplishes vital tasks.

A major development in zoological neurology in the last quarter century has been the discovery that many taxa of invertebrates have a large proportion of their nerve cells unique and identifiable in every specimen, making it possible, bit by bit, to piece together all or nearly all of the circuitry. This should apply at least as much to the zooplankters as to the bulky lobsters and sea slugs. Such encouragement, combined with the message documented above, that small size and slipperiness need not prevent microelectrode recording with controlled stimulation, makes it clear that the time is ripe and the technics available to make real inroads into this massive agenda. The clues and precedents from work already accomplished by pioneers in the area also make it clear that we can expect surprises and major discoveries, not simply smaller versions of familiar neuroethology. Zooplankton, in its marvellous variety, faces a set of problems in everyday living different from those of benthic, littoral and other faunas and not at all uniform or uneventful as we might imagine from our human perspective on their watery world. I look forward to the next convening of this range of specialists since it seems certain that in the interim this meeting will have sparked an abundance of new efforts and fascinating stories.

References

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