The University of Hawai'i at Manoa

SYMPOSIUM ON THE

SENSORY ECOLOGY AND PHYSIOLOGY

OF ZOOPLANKTON

January 8-12, 1995
Ala Moana Hotel
Honolulu, Hawaii

Organized by:

Petra H. Lenz, University of Hawai'i
Daniel K. Hartline, University of Hawai'i
Jennifer Purcell, University of Maryland System

Sponsored by:

Office of Naval Research
International Brain Research Organization
Pacific Biomedical Research Center, University of Hawai'i at Manoa
University of Hawai'i Sea Grant College Program
University of Maryland System, Center for Environmental and Estuarine Studies
Horn Point Environmental Laboratory

E-mail: **lucifer@wana.pbrc.hawaii.edu**

DEDICATION

This symposium is dedicated to the memory of
Dr. Mike S. Laverack,
Pioneer in the study of sensory structures in Crustaceans.

He never lost sight of the fact that the Class Crustacea includes many interesting animals besides lobsters, crayfish and crabs.

Dr. Laverack was involved in the initial stages of the planning of the symposium. Many of his ideas for topics and participants have been incorporated into the symposium plans.

ACKNOWLEDGEMENTS

The symposium started as a vague idea and a sense that most sensory biology meetings lack papers on zooplankton, and most zooplankton behavior conferences have few if any papers focused on sensory aspects. From these beginnings, many people have helped us in the evolution from idea to symposium. We would like to thank Dr. Randy Alberte, Office of Naval Research, Dr. Jack Davidson, University of Hawai'i Sea Grant College Program, Dr. Fred Greenwood, Director of Pacific Biomedical Research Center, Dr. Mike Laverack, Dr. David Macmillan, University of Melbourne, Dr. Gus Paffenhöfer, Skidaway Institute of Oceanography, Dr. Art Popper, University of Maryland, College Park, Prof. Dr. Piergiorgio Strata, International Brain Research Organization, and Prof. Dr. Konrad Wiese, Universität Hamburg.

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The staff at Pacific Biomedical Research Center, University of Hawaii generously supported the symposium through their time, advice and secretarial expertise. We would specially like to thank Mr. Dave Au, Administrative Officer, Dr. Marilyn Dunlap, Biological Electron Microscope Facility, Dr. Brad Jones, Békésy Lab. of Neurobiology, Ms. Carol Kosaki, Békésy Lab. of Neurobiology and Ms. Lynette Reyes, Békésy Lab. of Neurobiology.

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SYMPOSIUM PROGRAM

SUNDAY, JANUARY 8, 1995: REGISTRATION AND RECEPTION

1800-2000 Registration -- outside Garden Lanai

1800 No-host cocktail reception -- Garden Lanai

1830 Welcome - P. Lenz
Symposium Goals - D. Hartline
Introductions - J. Purcell

MONDAY, JANUARY 9, 1995: GENERAL

MORNING SESSION -- Garden Lanai

0825 Introduction - Chair: K. Wiese

SENSORY SYSTEMS

0830 J. Atema -- Spectral, temporal and spatial signals in nearfield and farfield chemoreception

0900 D. Mellon, Jr. -- Characteristics of broad spectrum neurons in crustacean olfactory midbrain

0920 T. Cronin, N.J. Marshall and R.L. Caldwell -- Compound eyes and photoreception in meroplanktonic crustacean larvae

0950 *Break* -- Garden Lanai (coffee, tea, breads)

1010 A.N. Popper -- Sound detection by fishes

1040 H. Bleckmann, J. Mogdans and A. Fleck -- Integration of hydrodynamic information in the hindbrain of fishes

1100 B. Schmitz -- Reception and production of hydrodynamic stimuli in crayfish and snapping shrimp

PELAGIC ENVIRONMENT - Physical aspects

1120 M.A.R. Koehl -- Hydrodynamics of olfactory antennae

1140 T. Breithaupt -- The structure and biological significance of water currents in predator-prey interactions and chemical communication

1200 *Lunch* -- Hibiscus Room

AFTERNOON SESSION -- Garden Lanai

1300 Introduction - Chair: D. Nilsson

PELAGIC ENVIRONMENT - Biological aspects

1305 *Video presentation*: J.R. Strickler -- Information, information, information! Seeing von Uexküll's "Umwelt" of planktonic crustaceans and the animal's reactions towards it

1335 D.E. Morse and A.N.C. Morse -- Signals, receptors, transducers and genes controlling substratum-specific metamorphosis: Larval ecology and practical applications

CRUSTACEAN MICRONEKTON

1405 J.F. Case -- No place to hide: Bioluminescence and the sensory ecology of pelagic crustaceans

1435 M.I. Latz -- Cryptic bioluminescence in the midwater environment

1455 M. Omori, H. Fukami and M.I. Latz -- Confirmation and measurement of bioluminescence of the pelagic shrimp *Sergia lucens*

1515 T.M. Frank and E.A. Widder -- Behavioral sensitivity to near-UV and blue-green light in deep-sea crustaceans

1535 K. Wiese -- Recording and analysis of the turbulent propulsion jet of euphasiid shrimp (Crustacea)

1555 *Break* -- Garden Lanai (coffee, tea)

ROTIFERS

1610 P.L. Starkweather -- Sensory potential in ciliated zooplankton: Structural and behavioral aspects of diet selection in rotifers

1635 T.W. Snell and R. Rico-Martinez -- Surface glycoproteins serve as contact mate recognition pheromones in rotifers

1655 D.J. Lonsdale, T.W. Snell and M.Frey -- Lectin binding to surface glycoproteins on *Coullana spp.* (Copepoda: Harpacticoida) can inhibit mate guarding

TUESDAY, JANUARY 10, 1995: PLANKTONIC CRUSTACEANS

MORNING SESSION -- Garden Lanai

0825 Introduction - Chair: P. Starkweather

0830 P. Larsson -- Behaviour and ecology of cladocera with focus on the influence of chemical signals in their environment

0900 J. Ringelberg and E. van Gool -- Memory for fish kairomone in *Daphnia* & E. van Gool and J. Ringelberg -- The influence of kairomones and food concentration on the response of *Daphnia* to changing light intensities

0930 L. DeMeester -- Qualitatively different responses of *Daphnia* clones to the presence of predator smell

0950 S.I. Dodson -- Optimal swimming behavior in zooplankton

1010 *Break* -- Garden Lanai (coffee, tea, pastries)

1030 D.-E. Nilsson -- Eye design, vision and invisibility in planktonic invertebrates

1100 N.J. Marshall and M.F. Land -- Orientation and tracking by hyperiid amphipods

1120 E.J. Buskey, J.O. Peterson, J.W. Ambler -- The role of photoreception in the swarming behavior of the copepod *Dioithona oculata*

1140 J.W. Ambler, S.A. Broadwater, E.J. Buskey, M. Kracht, and J.O. Peterson -- Mating behavior in swarms of *Dioithona oculata*

1200 Open discussion

1205 *Lunch* -- Hibiscus Room

1300 *SPECIAL LUNCHEON ADDRESS*
T.H. Bullock, Scripps Institution of Oceanography
Neuroethology and the aquatic realm

AFTERNOON SESSION -- Garden Lanai

1355 Introduction - Chair: J. Case

1400 J. Yen, S. Colin, M. Doall, P. Moore, A. Okubo and J.R. Strickler -- Mate tracking in copepods: Pheromones or species-specific wakes?

1420 S.M. Bollens, B.W. Frost, and J.R. Cordell - Individual behavioral flexibility of the marine copepod *Acartia hudsonica* in response to food and predators

1440 G.A. Boxshall, R. Huys, S. Ohtsuka, J.R. Strickler, and J. Yen -- The evolution of non-feeding males in marine planktonic copepods

1500 M.H. Bundy and G.-A. Paffenhöfer -- The sensory physiology of copepod nauplii investigated using laser scanning confocal microscopy

1520 D.K. Hartline and P.H. Lenz -- Sensory physiological studies of the first antenna of calanoid copepods

1540 Open discussion

1545 *Break* -- Carnation Room

1600-2130 Informal video presentations (by sign-up) -- Carnation Room

1600-1700 **POSTER PRESENTATIONS I** (posters go up by 0830; come down by 2200) -- Carnation Room

1a. K.B. Heidelberg, K.P. Sebens and J.E. Purcell -- Water flow effects on zooplankton escape behaviors from coral predators

1b. L.J. Hansson -- Behavioural responses to contact between the scyphozoan predator *Cyanea capillata* and the prey *Aurelia aurita*

2a. M. Brewer -- Virtual plankton: A novel method for investigating zooplankton predator-prey interactions

2b. J. Gokcen and D. McNaught -- Behavioral bioassays employing *Daphnia* for detection of sublethal effects: responses to polarized light

3a. N. Butler -- Effects of sediment loading on food perception and ingestion by freshwater zooplankton

3b. C.K. Wong, Q.C. Chen and L.M. Huang -- Responses of copepods to hydromechanical stimuli

WEDNESDAY, JANUARY 11, 1995: LARVAE

MORNING SESSION -- Garden Lanai

0825 Introduction - Chair: M. Koehl

MEROPLANKTON

0830 M. Hadfield -- Metamorphosis in marine invertebrates: The need for speed

0900 R. B. Forward, Jr. -- Sensory physiology and behavior of crab larvae during horizontal transport

0930 M.S. Laverack, D.L. Macmillan and S.L. Sandow -- Neural development in the planktonic and early benthic stages of the palinurid lobster, *Jasus edwardsii*

1000 *Break* -- Garden Lanai (coffee, tea, pastries)

1020 A.N.C. Morse and P.T. Raimondi -- The use of a novel chemo-inductive substrate resolves factors involved in recruitment of coral larvae

1040 R.K. Zimmer-Faust -- Chemosensory ecology of marine larvae: Benthic-pelagic coupling

MICRONEKTON

1110 B.U. Budelmann -- Cephalopod sensory neurobiology

1140 Open discussion

1200 *Lunch* -- Ilima Room

AFTERNOON SESSION -- Garden Lanai

1310 Introduction (Chair: B. Budelmann)

1315 H.I. Browman -- Sensitive periods in the neurobiological and behavioral development of fishes

1350 D. Featherstone, C. Drewes and J. Coats -- A technique for noninvasive detection of neural and muscular electrical events during the escape response in larval fish

1410 F.A. McAlary, E.R. Loew and W.N. McFarland -- Planktivory in larval fishes: Enhancement of foraging on zooplankton by ultraviolet sensitive vision

1430 Open discussion

1440 *Break* -- Carnation Room

1440-2130 Informal video presentations (by sign-up) -- Carnation Room
1530: Doall
1600: Fields
1630: Stewart

1440-1640 POSTER PRESENTATIONS II (posters go up by 0830; come down by 2200) -- Carnation Room

1440-1540 *Poster presentations IIa*

1a. M.H. Doall, J. Yen and J.R. Strickler -- Prey detection and attack performance in *Euchaeta rimana*, a predatory calanoid copepod (video 1530)

2a. D.M. Fields and J. Yen -- The escape behavior of marine copepods in response to quantifiable fluid disturbance (video 1600)

3a. L. Farley, T. Breithaupt and J. Atema -- A comparison of developmental changes in sensory anatomy and flow field dynamics between larvae and post-larvae of *Homarus americanus*

4a. I. Walter and K. Anger -- Delay of metamorphosis in decapod larvae due to substrate and conspecific cues

5a. T.P. Norekian -- Sensory inputs to the neurons underlying prey capture in the pteropod mollusc, *Clione limacina*

1540-1640 *Poster presentations IIb*

1b. E. van Gool and J. Ringelberg -- The influence of kairomones and food concentration on the response of *Daphnia* to changing light intensities

2b. C. Herren, P.H. Lenz and D.K. Hartline -- Behavioral responses of calanoid copepods to quantitative mechanical stimuli

3b. T. Weatherby and P.H. Lenz -- Morphological studies of mechano- and chemoreceptive setae in the first antenna of a calanoid copepod

4b. S. Stewart -- Field and laboratory observations of the cubozoan *Tripedalia cystophora*: implications regarding vision (video 1630)

5b. J. Arnold -- Title not available (cephalopod stereocilia)

1930 - 2030 **SPONSORS HOUR**
Office of Naval Research - Dr. Harold Bright
Sea Grant - Dr. Jack Davidson

THURSDAY, JANUARY 12, 1995: GELATINOUS ZOOPLANKTON

MORNING SESSION -- Garden Lanai

0825 Introduction - Chair: J. Purcell

CNIDARIANS & CTENOPHORES

0830 G.O. Mackie -- Involution, intimidation, escape: Defensive strategies in planktonic coelenterates

0900 W.M. Hamner -- Migration and spawning in cnidarians

0930 J.H. Costello, B.K. Sullivan and C.L. Suchman -- Prey responses to scyphomedusan flowfields -- do they explain prey selection?

0950 A.N. Spencer, N. Grigoriev and J. Przysiezniak -- Excitability properties of epithelia and neurons in *Polyorchis* (Hydrozoa): Their relevance to behavior

1010 *Break* -- Garden Lanai (coffee, tea, pastries)

1030 G. Matsumoto -- Observations on the anatomy and behaviour of the cubozoan *Carybdea rastonii*

1050 J.E. Purcell and P.A.V. Anderson -- Chemical basis for prey selection in a pelagic cnidarian

1110 T. Falkenhaug and O.B. Stabell -- Predator-prey interactions in ctenophores

1130 W. Greve -- Response patterns of a ctenophore: *Pleurobrachia pileus*

1150 Open discussion

1200 *Lunch* -- Hibiscus Room

AFTERNOON SESSION -- Garden Lanai

1310 Introduction - Chair: J. Purcell

CHORDATES

1330 L.P. Madin -- Sensory ecology of pelagic tunicates: More questions than answers

1400 G.O. Mackie -- Unconventional signalling mechanisms in pelagic tunicates

1430 J.-L. Acuña, D. Deibel and C.C. Morris -- Flow fields within the pharynx of an oikopleurid tunicate

1450 A.B. Bochdansky and D. Deibel -- Behavioral ecology of *Oikopleura vanhoeffeni* (Appendicularia)

1510 C. Galt -- Larvacean houses deter predation by fish and chaetognaths

PTEROPODS

1530 R.A. Satterlie, M. Lagro, M. Titus, S. Jordan and K. Robertson -- Morphology of wing mechano-receptors involved in the wing retraction reflex of the pteropod mollusc *Clione limacina*

1550 Open discussion

1600 *TEA PARTY* -- Garden Lanai

ABSTRACTS

FLOW FIELDS WITHIN THE PHARYNX OF AN OIKOPLEURID TUNICATE. J.-L. Acuña[1], D. Deibel[2] and C.C. Morris[2], [1]Departmento de BOS., University Oviedo, c/ Jesús Arias de Velasco (S/N), Oviedo 33005, Spain, and [2]Ocean Sciences Centre, Memorial University of Newfoundland, Canada

We have used video-assisted microscopy to track marker particles within the pharynx of *Oikopleura vanhoeffeni*. Our prime motivation was an attempt to rationalize two apparently contradictory results we have published, (1) that the pharyngeal filter of *O. vanhoeffeni* is relatively coarse (mean pore dimensions of 3.2 x 6.4 μm) and (2) that this filter appears to capture submicron particles with much higher efficiencies than can be accounted for by a sieving model.

Flow velocity was highly variable across the surface of the filter, with maximum particle impact velocities just above the ciliated spiracles. The mean impact velocity of particles we measured was 560±290 $\mu m\ s^{-1}$ (±SD, n=30). Thus, the Re number is 6×10^{-5} for a filter fiber 203 nm in diameter. The pharyngeal filter is made of rectilinear pores and operates in a closed system. Thus, it is an ideal case for application of the pressure drop and retention efficiency equations of Silvester (1983) derived from aerosol filtration theory. We used the pore dimensions and fiber diameter above, and the impact velocities we have measured, to predict retention efficiencies using Silvester's equation. Predicted values fall within the 95% confidence limits of empirically-determined retention for particles between 0.17 and 3 μm in diameter. Thus, direct interception accounts for the observed overcapture of very small particles less than the sieve dimensions.

MATING BEHAVIOR IN SWARMS OF *DIOITHONA OCULATA*. J.W. Ambler[1], S.A. Broadwater[1], E.J. Buskey[2], M. Kracht[1], and J.O. Peterson[2], [1]Millersville University, Millersville, PA 17551, USA[1]. [2]Marine Science Institute, University of Texas at Austin, Port Aransas, TX 78373, USA

The adaptive significance of dioithonan swarming may be to enhance mating behavior by bringing together many conspecific adults. Although light is the primary cue for initiating and maintaining swarms, chemical cues such as sex phermones may help maintain individuals in a swarm. We observed mating behavior of copepod pairs, and videotaped mating in laboratory swarms. Laboratory swarms of single stages and sexes were videotaped to determine if swarm formation and maintenance depended on the presence of adult females which are most photosensitive. Groups composed of only adult females, adult males, or copepodid stage 5 formed dense swarms, but younger copepodid stages did not. To observe conditions leading to mating interactions, we first created an all male swarm, added experimental animals (adult females, virgin females, C5, or males) to a screened compartment, and then raised the screen so that both groups formed a swarm. In all these experiments, mating was observed only between newly molted virgin females and males. Motion analysis did not reveal differences in average swimming behavior between the initial swarm with only males, and the later swarm with males and females mating. Therefore, premating swimming behavior did not appear to be different from swimming behavior in swarms. Swimming patterns of coupled pairs was distinctly different, and are being quantified.

SPECTRAL, TEMPORAL AND SPATIAL SIGNALS IN NEARFIELD AND FARFIELD CHEMORECEPTION. J. Atema, Marine Biological Laboratory, Boston University Marine Program, Woods, Hole, MA 02543, USA

For many animals, the world of immediate interest is only a few body lengths in size. Larger and faster animals have greater need for distance perception. Tactile, hydrodynamic and acoustic pressure signals represent a series of mechanical information channels covering increasing distances. Specific receptor organs cover the three distance ranges. A similar series exists in chemoreception. The ranges--contact, nearfield, farfield--are covered by a variety of receptor organs, such as taste and smell.

All chemical signals have in common the potential for precise identity information. This can include recognition of individuals and their internal state as well as subtly different food sources and home areas. Thus, spectral signal analysis is common to all chemoreceptor organs. In contact and nearfield chemoreception, temporal stimulus analysis is simple, but here spatial analysis across the body surface can be complex. In farfield chemoreception there is no brain body projection, but here temporal analysis of turbulently dispersed odor patches may be used to locate distant odor sources. Finally, functional and anatomical links between chemo- and mechanoreception are evident but poorly understood.

INTEGRATION OF HYDRODYNAMIC INFORMATION IN THE HINDBRAIN OF FISHES. H. Bleckmann, J. Mogdans and A. Fleck, Zoologisches Institut der Universität Bonn, Poppelsdorfer Schloβ, 53115 Bonn, Germany

Aquatic animals which move or which move body parts generate hydrodynamic stimuli which can have frequency components up to 100 Hz or more. Although hydrodynamic stimuli (near-field water displacements) attenuate rapidly during stimulus propagation due to the physical properties of water, they are of great interest to both, predators and prey. Fish use a special sensory system, the lateral line to detect weak water movements. The lateral line consists of up to several thousand individual neuromasts spread over the head and body. Lateral line neuromasts are mechanical low-pass filters which respond about proportional to either the velocity or the acceleration component of a wave stimulus. This holds true for frequencies from below 1 Hz up to about 150 Hz, i.e. up to the upper frequency limit of this sensory system. Within this frequency range, the stimulus parameters duration, amplitude, frequency, and phase are signalled to the brain. Here, we present data from electrophysiological recordings in the hindbrain of two fish species, a catfish, *Ancistrus sp.* and the goldfish, *Carassius auratus*. Our data demonstrate in which way different aspects of the hydrodynamic stimuli are processed by the hindbrain of fishes.

BEHAVIORAL ECOLOGY OF *OIKOPLEURA VANHOEFFENI* (APPENDICULARIA). A.B. Bochdansky and D. Deibel, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland, A1C 5S7, Canada

A new flow-through technique enabled us to measure the clearance rates and record the behavior of individual appendicularians simultaneously on video. Our direct measurements of the clearance rates support the Morris & Deibel - model (1993) which was based on behavioral and morphological studies on this species. Detailed time-budget analysis of the major components of the behavior (time spent feeding [TSF], tailbeat frequency [TBF] and the presence or absence of the pharyngeal filter), revealed that the 'feeding effort' is best described by the product of TSF and TBF. *O. vanhoeffeni* actively responded to an increased food concentration by reducing their feeding effort down to a certain threshold level. Further increase of food concentration resulted in a linear increase of the ingestion rates (determined by fecal pellet volume) with food concentration. In our experiments TSF varied by 10-fold (10-100%), whereas the TBF was bracketed within 0.6 to 1.3 tailbeats per second (2-4 degrees C). More variance in the clearance rates was explained by TSF than by size for animals varying from 2.16 to 5.6 mm in trunk length. Time intervals between fecal pellets was independent of the food concentration, suggesting constant gut passage times. However, the time interval between the egestion of fecal pellets changed dramatically when the animals ceased to produce the pharyngeal filter. The implications of our findings for particle fluxes in the sea and for the design of functional response experiments will be discussed.

INDIVIDUAL BEHAVIORAL FLEXIBILITY OF THE MARINE COPEPOD *ACARTIA HUDSONICA* IN RESPONSE TO FOOD AND PREDATORS. S.M. Bollens[1], B.W. Frost[2], and J.R. Cordell[3], [1]Biology Department, Woods Hole Oceanographic Institute, Woods Hole, MA, 02543 [2]School of Oceanography, WB-10, University of Washington, Seattle, WA 98195, [3]Fisheries Research Institute, WH-10, University of Washington, Seattle, WA 98195, USA

We present results from a suite of experimental studies investigating if individual *A. hudsonica* possess flexibility in their habitat (depth) selection behavior. A series of manipulation experiments were undertaken in a temperate marine lagoon in which we varied the concentration of both predators and food resources in well-replicated, *in situ* plastic enclosures spanning the natural depth range of the copepods. We review briefly some of our previously published results indicating that adult female *A. hudsonica* can respond to the presence or absence of their natural predator, the threespine stickleback (*Gasterosteus aculeatus*), by altering their diel vertical migration behavior and their diel cycle of feeding. More recent, unpublished results are presented indicating that *A. hudsonica* can also alter their vertical distribution in response to variable food resources. These results are discussed in the context of individual zooplankters making trade-offs between predator avoidance and feeding in their habitat selection behavior.

THE EVOLUTION OF NON-FEEDING MALES IN MARINE PLANKTONIC COPEPODS. G.A. Boxshall[1], R. Huys[1], S. Ohtsuka[2], J.R. Strickler[3], and J. Yen[4], [1]The Natural History Museum, London SW7 5BD, London, U.K. [2]Fisheries Laboratory, Hiroshima University, 1294 Takehara-cho, Hiroshima 725, Japan. [3]Center for Great Lakes Research, University Wisconsin-Milwaukee, 600 E. Greenfield Ave., Milwaukee, WI 53204, USA. [4]Marine Sciences Research Center, State University of New York, Stony Brook, NY 11974-5000, USA

Non-feeding adult males with atrophied mouthparts are more widespread amongst the marine planktonic copepods than hitherto realised. Phylogenetic analysis indicates that this phenomenon has evolved independently on numerous occasions and examples can be found in five different orders: Calanoida, Harpacticoida, Poecilostomatoida, Siphonostomatoida and Mormonilloida. The extent of the degeneration in mouthpart structure varies from group to group but a common pattern can be recognized. The cessation of feeding at the final moult from fifth copepodid to adult male is also marked by profound changes in the array of sensors carried along the paired antennules. Some of these changes are correlated with the cessation of feeding but comparative studies indicate that other changes are linked to the onset of sexual maturity and, in particular, to mate location behaviors.

THE STRUCTURE AND BIOLOGICAL SIGNIFICANCE OF WATER CURRENTS IN PREDATOR-PREY INTERACTIONS AND CHEMICAL COMMUNICATION. T. Breithaupt, Universität Konstanz, Fakultät für Biologie, Postfach 5560 (M 618), D-78434 Konstanz, Germany

Hydrodynamic receptor systems have been described and studied in detail in a variety of aquatic organisms, including crustaceans. Little is known, however, about the physical parameters of the stimuli to which they have adapted. Using modern techniques (laser anemometry, flow visualization) flow fields were investigated that are created by swimming and breathing animals and that, in natural contexts, are detected and processed by hydrodynamic receptor systems. Swimming fish (cave fish *Astyanax fasciatus* and the trout *Salmo gairdnerii*) create a laminar flow field around the head region (bow wave). Every tail beat, in contrast, evokes strong turbulent water disturbances that detach from the fish and travel, for a considerable distance and time, through the water in the form of stable vortex rings. Behavioral studies indicate that blindfolded crayfish (*Procambarus clarkii*), catching small fish, use both bow waves and vortex rings for hydrodynamic orientation. Water currents can also convey chemical information about the sources of disturbance. Lobsters (*Homarus americanus*) use self generated currents both for breathing and for the dispersal of their urine. Urine borne pheromones are used by conspecifics to recognize the dominant animal from previous fights. Detailed study of flow patterns and pheromone release revealed a sophisticated apparatus for the directional and temporal control of chemical signals. This example reflects the tight coupling between chemical and hydrodynamic stimuli.

"VIRTUAL PLANKTON": A NOVEL METHOD FOR INVESTIGATING ZOOPLANKTON PREDATOR-PREY INTERACTIONS. M.C. Brewer, Center for Great Lakes Studies, University of Wisconsin-Milwaukee, 600 E. Greenfield Ave., Milwaukee, WI 53204, USA

The conservative swimming hypothesis (CSH) states that individual *Daphnia* swimming behavior has evolved to maximize fitness in the presence of predators. Numerous chemical and physical environmental cues combine to shape *Daphnia*'s swimming behavior at any moment. Specifically, the CSH predicts that a *Daphnia*'s swimming behavior relative to the behavior of other members of the population affects predation risk. Individuals that swim in a manner that differs from their neighbors become more conspicuous to visually cued planktivorous fish and therefore, more vulnerable to predation.

This prediction was tested using computer simulated "virtual *Daphnia*". Individual fish were trained to attack small dots on a computer monitor that moved in a manner that mimics *Daphnia*'s hop-and sink swimming behavior. This system was used to test the hypothesis that fish show a preference for individual virtual *Daphnia* that swim differently from a background "population" of other virtual *Daphnia*.

SENSITIVE PERIODS IN THE NEUROBIOLOGICAL AND BEHAVIOURAL DEVELOPMENT OF FISHES. H.I. Browman, Department of Fisheries and Oceans Canada, Maurice-Lamontagne Institute, Marine Productivity Division, 850 Route de la Mer, P.O. Box 1000, Mont-Joli, Québec, G5H 3Z4, Canada

An overview of neurobiological and behavioural development in fishes will be presented. Since it would be impossible to provide details for every sensory system and/or behaviour in the time available, vision and visually-guided foraging behaviour will be emphasized. The manner in which the developmental trajectory presented for the visual system can be generalized to other sensory modalities will be evaluated. The concept of ontogenetic sensitive periods (SPs), which have been defined at several different biological levels, will be used as an example of the possible interactions between a fish's neuroethological development and its ecology. For the purposes of this discussion, SPs represent restricted and discrete temporal windows during which an animal's developing organ systems are particularly susceptible to environmental influences. It is asserted that SPs at different biological levels - embryological, neurobiological, ethological and ecological - are hierarchically interrelated. If this is so, the environmental conditions to which a fish is exposed during its development may have fundamental consequences for how it transduces sensory information and, therefore, for how it behaves.

CEPHALOPOD SENSORY NEUROBIOLOGY. B.U. Budelmann, Marine Biomedical Institute and Department of Otolaryngology, University of Texas Medical Branch, Galveston, TX 77555-0863, USA

Cephalopods are the most highly evolved invertebrates. With only a few exceptions, they are visually oriented, fast moving predators with highly effective sense organs and a sophisticated brain. The degree of complexity of these systems differs in the various cephalopod groups, depending upon the demands of their lifestyle and the environment in which they live. This paper will briefly outline the structure, function and biological significance of the sense organs cephalopods possess, as well as highlight some of the capabilities of their nervous system. Special emphasis will be placed on their vertebrate-like eyes which, most likely, do not see colors but, instead, the plane of polarized light; their vestibular analogue statocysts with receptor systems for linear and angular accelerations; their control system for compensatory eye movements which is similar to the vertebrate vestibulo-oculomotor reflex (VOR); their lateral line analogue system; the question whether or not cephalopods can hear; their touch and distant chemoreceptors; their recently discovered neck proprioceptor organ which monitors the position of the head relative to the body; and their highly centralized nervous system which is capable of different forms of learning and memory.

THE SENSORY PHYSIOLOGY OF COPEPOD NAUPLII INVESTIGATED USING LASER SCANNING CONFOCAL MICROSCOPY. M.H. Bundy[1] and G.-A. Paffenhöfer, Skidaway Institute of Oceanography, 10 Ocean Science Circle, Savannah, GA 31411. USA. ([1]Present address: Great Lakes Environmental Research Laboratory, NOAA, 2205 Commonwealth Blvd., Ann Arbor, MI 48105, USA)

The functional morphology of the first and second antennae (A1 and A2) of the nauplius IV of the calanoid copepods *Eucalanus pileatus* and *Centropages velificatus* was investigated using laser scanning confocal microscopy (LSCM). *E. pileatus* nauplii create feeding currents and move constantly, while *C. velificatus* nauplii do not create a feeding current and move in intermittent jumps. The roles of mechanoreceptive and chemoreceptive sensilla on the A1 and A2 of the nauplius are discussed in terms of the remote detection of food particles and the control of swimming behavior.

THE ROLE OF PHOTORECEPTION IN THE SWARMING BEHAVIOR OF THE COPEPOD *DIOITHONA OCULATA*. E.J. Buskey, J.O. Peterson and J.W. Ambler, The University of Texas at Austin, Marine Science Institute, Port Aransas, TX 78373, USA

The copepod *Dioithona oculata* forms dense swarms near mangrove prop roots that are centered around shafts of light penetrating the mangrove canopy. These swarms form at dawn and disperse at dusk, and light seems to be an essential cue for swarm formation. *In situ* and laboratory observations of swarming behavior were recorded using video cameras, and the swimming behavior of the copepods and density of the swarms were quantified using video-computer motion and image analysis techniques. Swarms can be created in the laboratory under light shafts created with fiber optics. Swarm formation can occur at light intensities as low as 0.1 μmol photons $m^{-2}s^{-1}$. Copepods reverse their swimming direction when they encounter light intensity gradients near the edge of a light shaft, maintaining the swarm. Swarm formation appears to have an endogenous rhythm, as copepods will not form swarms at night under a light shaft. *In situ* observations of swarms indicate that densities of copepods in swarms can exceed 80 copepods ml^{-1}. Swarms can be maintained even during period when tidal currents exceed 2 cm s^{-1}, so that these 0.8 mm in length copepods sustain swimming speeds of >25 body lengths s^{-1} for periods of hours. Swarm formation may protect the copepods from predation by planktivorous fish by allowing them to maintain their position within the mangrove prop root habitat. Planktivores were rarely observed under the mangrove canopy, which is often populated with piscivorous fish.

EFFECTS OF SEDIMENT LOADING ON FOOD PERCEPTION AND INGESTION BY FRESHWATER ZOOPLANKTON. N.M. Butler, Flathead Lake Biological Station, The University of Montana, 311 Biostation Lane, Polson, MT 59860, USA

Suspended inorganic sediments, such as clays and silts, are an important non-point source of pollution in aquatic systems throughout the world. In the lakes of western Montana, the intensity of sediment loading is strongly influenced by land use patterns. The presence of suspended particles can affect not only the net primary productivity, as light penetration and the euphotic zone are reduced, but can also affect the availability of food to the herbivorous zooplankton. The majority of research on the effects of sediment loading on zooplankton feeding have centered on organisms which are not naturally associated with turbid environments. In Swan Lake, an oligotrophic lake located in northwestern Montana, there is a close association between zooplankton population development and seasonal maxima in turbidity levels, suggesting that the community present in the lake during peak turbidity levels is minimally impacted by the presence of suspended sediments. Here I present the results of laboratory investigations into the effect of suspended sediments on feeding by the copepod *Leptodiaptomus ashlandii*, the dominant zooplankter in Swan Lake. Using ^{32}P labeled algae (*Chlamydomonas reinhardtii*) offered in clay suspensions over of a range of 0 to 250 NTU's, I have observed that even at very low levels of turbidity (less than 25 NTU), the presence of suspended particles has a negative impact on feeding behavior and ingestion.

NO PLACE TO HIDE: BIOLUMINESCENCE AND THE SENSORY ECOLOGY OF PELAGIC CRUSTACEANS. J.F. Case, Marine Science Institute and Department of Biological Sciences, University of California, Santa Barbara, CA 93106, USA

The pelagic environment is a continuum lacking fixed points of reference except gravity, downwelling light and temperature transitions. It is transparent and almost universally lacks concealment. Micronecton numbers are low. Most micronecton faunal biomass is constituted of bioluminescent animals. Prominent among these are euphausids, mysids and decapods. While chemo- and mechanoreception are well developed in all these, the physics of the environment argues that vision coupled with bioluminescence dominates their long range interactions. Bioluminescence is important in tracking targets, even non-luminescent ones, by their triggering of third-party luminescence; it offers counterillumination concealment in appropriately lit depths; it probably provides signalling among conspecifics; and it might allow rapid estimation of local faunal structure, for example during vertical migration when predator/prey numbers at various depths are critically valuable information. The interplay of vision and bioluminescence in both predation and concealment will be discussed on the basis of investigations of compound eye physical optics, electrophysiological characterization of compound eye receptive fields, behavioral experiments, and field observations.

PREY RESPONSES TO SCYPHOMEDUSAN FLOWFIELDS -- DO THEY EXPLAIN PREY SELECTION? J.H. Costello[1], B.K. Sullivan[2] and C.L. Suchman[2], [1]Providence College, Providence RI 02918 and [2]University of Rhode Island, Narragansett, RI 02882, USA

In situ time budgets demonstrate that three species of scyphomedusae, *Aurelia aurita, Cyanea* sp. and *Chrysaora quinquecirrha*, spend 95-98% of their time swimming. Fluid motions created during swimming entrain prey and bring them to capture surfaces. However, *in situ* prey selection differs for the three species. We discuss relationships between predator flow field characteristics, prey swimming and escape patterns and prey selection by each species.

COMPOUND EYES AND PHOTORECEPTION IN MEROPLANKTONIC CRUSTACEAN LARVAE. T.W. Cronin[1], N.J. Marshall[2], and R.L. Caldwell[3], [1]University of Maryland, Baltimore Co , Baltimore MD 21228 USA; [2]Sussex University, Falmer, Brighton BN1 9QG UK; [3]University of California, Berkeley, CA 94720, USA

Larvae of stomatopod and decapod crustaceans possess paired compound eyes similar to those of adults of the same species. Such larvae are generally planktonic (for larvae, the term is "meroplanktonic") and predatory, and thus face the usual demands of making a living in the plankton. Their compound eyes are used for orientation, migration, and shadow avoidance. While there is at present no compelling evidence for their involvement in visual tasks requiring imaging, analogies with permanently planktonic crustaceans suggest that the behavior served by larval vision could be very complex. Since crustacean larvae pass through several developmental stages, and finally metamorphose to a very different adult form, larval compound eyes must change radically throughout development. They typically increase in size and in ommatidial number with each larval molt. In some species, ommatidial optics are fundamentally altered at metamorphosis. Most dramatically, in stomatopods, larval eyes are so different from the eyes of the postlarvae (and adults) that in a single metamorphic molt, the larval retina is replaced with an entirely new adult-type photoreceptor array.

QUALITATIVELY DIFFERENT RESPONSES OF *DAPHNIA* CLONES TO THE PRESENCE OF PREDATOR SMELL. L. De Meester, Laboratory of Animal Ecology, University of Gent, K.L. Ledeganckstraat 35, 9000 Gent, Belgium

The responses of *Daphnia* to the presence of predators (e.g. fishes) that have been reported in the literature include several behavioral (e.g. phototactic behavior, overall excitation, aggregation) and life history traits (e.g. size at maturity). It is suggested that showing all responses together may be maladaptive, at least under certain circumstances, and that the responses to the presence of predator-mediated chemicals may be clone-specific qualitatively in addition to quantitatively.

A comparison of the results on changes induced by the presence of fish-mediated chemicals in two behavioral characteristics, phototactic behavior and overall excitation, of *Daphnia* clones isolated from contrasting habitats, indeed indicates that the two responses are to some extent uncoupled. A hypothetical receptor-effector pathway is proposed to account for genetic differences in both nature and degree of the response to the presence of specific predators. It is noted that our results also imply that the observation of an absence of a specific response to the presence of a predator in a given *Daphnia* clone not necessarily is proof of the absence of functional receptors for kairomones released by that predator.

PREY DETECTION AND ATTACK PERFORMANCE IN *EUCHAETA RIMANA*, A PREDATORY CALANOID COPEPOD. M.H. Doall[1], J. Yen[1], and J.R. Strickler[2], [1]Marine Sciences Research Center, State University of New York at Sony Brook, Stony Brook, NY 11794-5000, USA. [2]Center for Great Lakes Studies, University of Wisconsin-Milwaukee, Milwaukee, WI 53208, USA

The sensory and attack performance of *Euchaeta rimana*, a predatory calanoid copepod, is assessed through behavioral analyses of interactions with smaller calanoid species. Predator/prey interactions are categorized based on the behavioral response and capture success of the predator, *E. rimana*. Three categories of interaction are defined: 1) escape, in which *E. rimana* fails to recognize the stimulus as prey and jumps away from it; 2) attack and miss, in which *E. rimana* recognizes and attacks (i.e., lunges toward) a prey item but does not successfully capture it; and 3) attack and capture, in which *E. rimana* recognizes and successfully captures a prey. Prey recognition efficiency is computed as the number of attack attempts divided by the total number of interactions. Attack efficiency is computed as the number of successful captures divided by the number of attack attempts. Preliminary analyses indicate that *E. rimana* can perceive a prey outside of its attack volume, and accelerate toward the three-dimensional location of the prey until within striking distance. The attack volume of *E. rimana* is described by plotting prey locations at the moment of attack around a standard three-dimensional orientation of *E. rimana*.

OPTIMAL SWIMMING BEHAVIOR IN ZOOPLANKTON. S.I. Dodson, Department of Zoology, University of Wisconsin, 430 Lincoln Drive, Madison WI 53706 USA

The Conservative Swimming Hypothesis (CSH) places zooplankton swimming behavior within an ecological and evolutionary context:

> zooplankton exhibit conservative swimming behavior over a wide range of environmental conditions. We hypothesize that conservative swimming is the result of a balance of adaptive ecological strategies that optimize fitness in the presence of predators.

The CSH synthesizes previous information (especially for freshwater zooplankton such as *Daphnia*) from different fields of freshwater ecology: chemical communication, feeding behavior, predator-prey encounter rates, predator sensitivity to variability in swimming activity, and synergisms among independent physical and biological factors. The CSH uses knowledge about both feeding and predator-prey ecology to make predictions about zooplankton swimming behavior over a wide range of interacting physical and biological conditions.

Testable predictions of a graphical model of the CSH include: 1) Individual swimming behavior affects feeding and population growth rates, 2) Food concentrations and predator encounter rates interact to produce conservative swimming, 3) Food concentration, above starvation levels, will not affect swimming behavior, 4) Uniform (low-variance) swimming behavior is a defense against visual predators, and 5) There are non-linear (synergistic) interactions between light level and predator smell (kairomone concentration).

PREDATOR-PREY INTERACTIONS IN CTENOPHORES. T. Falkenhaug and O.B. Stabell, The Norwegian College of Fishery Science, University of Tromsø, Tromsø, Norway

Two species of ctenophores coexist in the north-east Atlantic, one (genus *Bolinopsis*) forages crustaceans, while the other (genus *Beroe*) feeds exclusively on the former. In laboratory experiments, *Bolinopsis* demonstrated an escape response to mechanical stimuli directed towards the frontal lobes; while chemical stimuli, in the form of water conditioned by the predator, gave no detectable responses. Physical contact with a predator, observed in experiments as a direct touch between the sides of *Bolinopsis* and the rear end of *Beroe*, initiated no flight response. No detectable increase in search behaviour by *Beroe*, measured as swimming activity, could be found, neither when stimulated with water conditioned by *Bolinopsis*, nor when stimulated with extracts of homogenised specimens of the prey. *Beroe* turns towards a prey, however, as a result of a mechanical stimulus on the sides of the body, probably initiated by wake of a passing prey, as demonstrated by weak water jets from pipettes. Jets of water conditioned by *Bolinopsis* caused no increase in the turning response. Turning towards a prey mostly resulted in direct contact by the 'lips', further initiating a rapid feeding response by extension of the mouth opening, and ingestion of the prey by sucking. The importance of chemical stimuli in the final stage of prey selection was confirmed by lack of mouth extension following contact with glass pipettes, whereas mouth extension and feeding behaviour, directed towards the wall of a glass jar, was observed when tissue from *Bolinopsis* was squeezed between the mouth opening and the wall of the jar.

COMPARISON OF DEVELOPMENTAL CHANGES IN SENSORY ANATOMY AND FLOW FIELD DYNAMICS BETWEEN LARVAE AND POST-LARVAE OF *HOMARUS AMERICANAS*. L.G. Farley[1], T. Breithaupt[2], and J. Atema[1], [1]Boston University Marine Program, Woods Hole, MA 02543, USA, [2]University of Konstanz, D-78434 Konstanz, Germany

After hatching, the lobster *Homarus americanus* has three pelagic larval stages (I-III) and one transitional post-larval stage (IV) before settling into a benthic existence. Morphologically, larvae are mysid shaped, and have feathery exopodites on the thoracic appendages that are capable of generating currents. The metamorphic molt occurs between stage III (larva) and stage IV (post-larva), where there is a transition from the mysid shape to the adult lobster morphology. During the post-larval stage, the thoracic exopodites are regressed and the pleopods of the abdomen are used for swimming. Very little is known about how larval and post-larval stages obtain sensory information from their respective environments. Since currents which pass over the lateral antennule may contain sensory information, both the sensory anatomy of the lateral antennule and the flow field dynamics of the currents are being examined. The stage I lateral antennule (the organ of olfaction in the adult lobster) does not possess chemosensory aesthetasc sensilla, but instead possesses a large distal giant sensillum. Anatomical studies using DIC microscopy showed that the presumptive nerve fibers at the base of the giant sensillum develop into aesthetasc sensilla. This provides preliminary evidence that the giant sensillum may be chemosensory sensillum. In addition to anatomical studies, comparative flow field analyses were performed on larval stages I-III and post-larval stage IV to examine the possible information/feeding currents produced by each stage. During the larval stages, the thoracic exopodites produce currents which are capable of drawing particles from the posterior as well as particles anterior over the antennules and mouthparts. The post-larvae generate very powerful pleopod currents by which they direct the flow from anterior to posterior. From the flow field analyses, it appears that larvae and post-larvae generate currents which would allow for chemicals to encounter chemoreceptive organs and these currents may also increase prey encounters, as is known for post-larval stages.

A TECHNIQUE FOR NONINVASIVE DETECTION OF NEURAL AND MUSCULAR ELECTRICAL EVENTS DURING THE ESCAPE RESPONSE IN LARVAL FISH. D. Featherstone[1], C. Drewes[2], and J. Coats[3], [1]Békésy Laboratory of Neurobiology, Pacific Biomedical Research Center, University of Hawaii, Honolulu, HI 96822, [2]Department of Zoology, Iowa State University, Ames, IA 50011, USA., [3]Department of Entomology, Iowa State University Ames, IA 50011, USA

In most teleost fish, an escape response occurs when a sudden stimulus (via one or several sensory modalities) causes one of a pair of Mauthner (M-) cells in the fish hindbrain to fire a single action potential. This action potential, as it travels tailward within the spinal cord, excites motor neurons which, in turn, activate axial muscle. We present a noninvasive electrophysiological technique for measuring, in intact larval fish, the following escape-related parameters: 1) The conduction velocity of the Mauthner spike as it travels caudally within the spinal cord. 2) Time from delivery of a standardized acoustical and vibrational stimulus to Mauthner spike initiation. 3) Delay time from Mauthner axon spike to motoneuron potential. 4) Probability of an escape behavior in response to a stimulus. 5) Electromyographic burst number and duration (representing the initial, fast body bend of the fish as it turns away from the stimulus, and subsequent tail flips as it swims away.) This technique may be useful for developmental, toxicological, or neurobehavioral studies which require repeated measurements on the same animal.

THE ESCAPE BEHAVIOR OF MARINE COPEPODS IN RESPONSE TO A QUANTIFIABLE FLUID DISTURBANCE. D.M. Fields and J. Yen, Marine Science Research Center, State University of New York, Stony Brook, NY 11794-5000 USA

Copepods are subject to high predation rates throughout much of their planktonic life. As a result predator detection and avoidance are crucial to the survival of individuals. This study examines the escape reaction of 4 oceanic species of copepods (from a variety of different habitats) in response to a quantifiable fluid dynamic disturbance. Of the animals studied one species (*Pleuromamma xiphias*) shows an extensive vertical migration being found between 20 meters during the night and 700 meters by day. Two other species, *Euchaeta rimana* and a cyclopoid copepod, are offshore surface dwellers while *Labidocera madurae* is found primarily at the surface in shallow waters. Fluid characteristics such as shear, velocity and acceleration rates at the point of escape are examined and compared for the different species. Preliminary data suggests that spatial variation in fluid velocity is most predictive of the escape location, however, each species had a different threshold that elicited the escape reaction.

Once initiated the escape reaction for all the species was extremely rapid. For the larger animals studied the escape speed surpassed 1000 mm/s with acceleration rates up to 14 times the acceleration due to gravity. The variability in stimulus threshold and escape speed between the different species may be a reflection of the different predation pressures on these animals.

SENSORY PHYSIOLOGY AND BEHAVIOR OF CRAB LARVAE DURING HORIZONTAL TRANSPORT. R.B. Forward, Jr., Duke University Marine Laboratory, Beaufort, NC 28516, USA

Many estuarine decapod crustaceans release their larvae at specific times relative to environmental cycles. They are then transported out of the estuary and undergo development in coastal areas. Using the blue crab *Callinectes sapidus* as an example, aspects of the sensory physiology and behavior involved in transport back to the adult habitat by the postlarval stage (megalopa) will be considered. Field studies indicate transport onshore to the mouth of an estuary is by wind generated surface currents, while selective tidal-stream transport is used for up-estuary movement. Chemical cues in offshore and estuarine waters induces separate behavioral responses to environmental factors which underlie onshore and up-estuary transport. A biological rhythm in activity and photoresponses maintain megalopae near the surface for onshore transport during the day. During up-estuary transport megalopae are in the water column during the rising tides at night and are on, or close to, the bottom at all other times. The ascent during rising tides could result from a tidal rhythm in activity or behavioral responses to changes in environmental factors such as temperature, pressure and salinity. Responses to these factors are frequently used for depth regulation among zooplankton. A consideration of the activity rhythm, and the physiology of responses to environmental factors indicates that the ascent is cued by the rate of change in salinity.

BEHAVIORAL SENSITIVITY TO NEAR-UV AND BLUE-GREEN LIGHT IN DEEP SEA CRUSTACEANS. T.M. Frank and E.A. Widder, Harbor Branch Oceanographic Institution, Ft. Pierce, FL 34946, USA

Several species of deep-sea crustaceans possess unusually high spectral sensitivity to near-UV light, measured electrophysiologically, in addition to the expected spectral sensitivity peak in the blue-green. A protocol was developed to determine if these species exhibited behavioral sensitivity to near-UV light as well. Experiments were conducted on 6 species of deep-sea crustaceans--3 pulative dichromats with the two spectral sensitivity peaks, and 3 putative monochromats, with a single peak in the blue-green. These experiments were conducted 1) to determine if there were behavioral differences to light between putative dichromats and monochromats, and 2) to measure and compare behavioral thresholds to long and short wavelength light. Results indicate that 1) there are no wavelength specific behaviors, and 2) that the putative dichromats are equally sensitive to near-UV and blue-green light, while the monochromats are almost a log unit less sensitive to near-UV vs. blue-green light. The possible functional significance of this unusual sensitivity to near-UV light in deep-sea organisms as it relates to vertical migration and bioluminescence will be discussed.

LARVACEAN HOUSES DETER PREDATION BY FISH AND CHAETOGNATHS. C. Galt, Department of Biological Sciences, California State University, Long Beach, CA 90840-3702, USA

Oikopleurids, frequent prey of zooplankton and fish, occupy renewable, mucous, feeding houses. Do larvacean houses also deter predation? I examined larvaceans' behavioral responses to visual predators (juvenile fish, to 4 cm long) and non-visual predators (chaetognaths, to 1.3 cm). As prey I used *Oikopleura longicauda* up to 1.2 mm body length and 5 mm house diameter. Both predator types readily detected and ingested *O. longicauda* when it swam freely without a house. Detection range was a few mm for chaetognaths, which detect the prey's rapid swimming vibrations, and more than 10 cm for visual fish. In contrast, chaetognaths did not strike at occupied houses, presumably because the gentle beating of the larvacean's tail provided insufficient sensory stimulus. Juvenile fish showed four interactions with occupied houses: (A) small fish pecked at but failed to disturb occupied houses; (B) larger fish pecked at the house, triggering an escape response in which the entire occupied house rolled away; (C) some fish attacked the house, yet *O. longicauda* rapidly exited the house and swam away; (D) some fish ingested the occupied house, then rapidly and invariably regurgitated it, while retaining the larvacean. Oikopleurids occupying houses are protected from predation in a variety of ways compared to highly vulnerable, free-swimming larvaceans.

BEHAVIORAL BIOASSAYS EMPLOYING *DAPHNIA* FOR DETECTION OF SUBLETHAL EFFECTS: RESPONSES TO POLARIZED LIGHT. J. Gokcen and D. McNaught, Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, USA

The swimming responses of *Daphnia pulicaria* to both polarized white and UV light were examined. Both sets of responses were employed as behavioral bioassays to investigate the effects of sodium bromide (NaBr) on their physiology. NaBr was chosen because it may be used in the Laurentian Great Lakes to eradicate the zebra mussel. The control responses to polarized light involved an orientation at 90° to the e-vector. With the addition of NaBr the response became random. An EC_{50} of 9.9×10^{-4} M NaBr was calculated, using the statistic Raleigh's Z to determine the significance of the plane of orientation. In contrast, the control response to polarized UV light was a random orientation to the e-vector. However, as NaBr concentrations increased, *Daphnia* began to exhibit repetitive behavior. At both 10^{-4} and 10^{-3} M NaBr, the organism consistently oriented itself between 0-60° to the e-vector of polarized light. An EC_{50} of 3.0×10^{-5} M NaBr was calculated for this response. A possible mechanism to account for the toxicity of this mild sedative is the blocking by the bromide ion of chloride channels involved in transmitting impulses.

THE INFLUENCE OF KAIROMONES AND FOOD CONCENTRATION ON THE RESPONSE OF *DAPHNIA* TO CHANGING LIGHT INTENSITIES. E. van Gool and J. Ringelberg, University of Amsterdam, Department Aquatic Ecology, Kruislaan 320, 1098 SM Amsterdam, The Netherlands

Diel vertical migration (DVM) of plankton animals like *Daphnia* is considered a strategy to diminish predation, for instance, by visual predators like juvenile fish. Disadvantages are low temperatures and low food concentrations at greater depth and models predict that the change in fitness depend on food availability and predation pressure. The amplitude of DVM is very variable, indeed. So it was hypothesized that *Daphnia* has a mechanism to decide whether to migrate or not, depending on the value of both factors. A first step was to quantify the influence of fish kairomones and food concentration on phototaxis. This phototaxis is considered the basic behaviour of migration. As a stimulus, the maximum relative increase in light intensity prevailing at sunrise was used and parameters such as the percentage of responding animals, displacement velocity, and latent period were determined. We found a significant influence of kairomones and food availability on the percentage of responses and on the latent period.

RESPONSE PATTERNS OF A CTENOPHORE: *PLEUROBRANCHIA PILEUS*. W. Greve, Biologische Anstalt Helgoland, Zenale Hamburg, 22607 Hamburg, Germany

The tentaculate ctenophore *Pleurobrachia pileus* is a highly successful species. Since 400 million years (the lower Devonian period) its organization seems to have remained almost unchanged. This may be due to the simple and efficient way in which its response patterns help to save energy and avoid destruction. The responses of *P. pileus* are organized on several hierarchical levels. These levels are:

the whole organism
the single tentacle as a complex of organs
the single organ

Within these levels, at least 31 discrete sensory responses and reactions can be discriminated. A detailed flow diagram of the behavioral responses has been determined and documented in a scientific film. Special attention is given to the synchronous and asynchronous handling of the tentacles. This may be an important means to save energy. The prey-catching behavior thus has been documented in 17 parallel phases. The responses to vibrations, scyphomedusan stinging, contact with *Beroe gracilis*, pressure changes, temperature changes, and other possible cues are demonstrated and discussed.

METAMORPHOSIS IN MARINE INVERTEBRATES: THE NEED FOR SPEED. M.G. Hadfield, Kewalo Marine Laboratory, Pacific Biomedical Research Center, University of Hawaii, Honolulu, HI 96822, USA

Accumulating evidence supports a hypothesis that external, chemically sensitive excitable cells initiate metamorphosis in swimming larvae of most benthic marine invertebrate species. The current model states that specific molecular receptors on the cell surfaces, upon exposure to threshold levels of specific external ligands, produce depolarization of the cell membrane, and the electrical stimulus is transmitted to responding tissues through the nervous system. Support for this hypothesis comes from (1) the rapidness of the metamorphic response, (2) the metamorphic stimulatory or inhibitory activity of known neuro-active agents, including a positive response to excess potassium ion in the medium, and (3) demonstration of altered electrical patterns in the brain of an invertebrate larva. For the larva to respond so rapidly to external chemical stimulation, it must be exceptionally "prepared" for metamorphosis, a criterion that is met by the development of metamorphic competence. Competent larvae need only nervous stimulation to commence metamorphosis. Great congruity of a phenomenon across a group of organisms is usually explained by evolutionary homology. However, the diversity of phyletic lineages and larval types demonstrating chemoreception-neurostimulation of metamorphosis make homology highly unlikely. Rather, the time of settlement and metamorphosis is probably the most vulnerable in the lifespan of marine invertebrate animals, and convergent evolution of neuro-stimulated metamorphosis has been nature's repeated response to this "need for speed."

MIGRATION AND SPAWNING IN CNIDARIANS. W.M. Hamner, Department of Biology, University of California, Los Angeles, CA 90024-1606, USA

Maintenance of persistent populations of meroplanktonic organisms over time requires that the planktonic phase of the life cycle return to the site of initial fertilization in spite of oceanographic factors that promote dispersion. For cnidarians with benthic larvae and planktonic adults, the medusae must not only return to a site suitable for larval settlement, but they must also return simultaneously in numbers sufficiently large so that planktonic spawning is possible. Spawning is often accomplished within highly aggregated masses of sexually mature medusae. Spawning, therefore, requires the neurological equipment both for returning to a specific location at sea and for recognizing the presence of other reproductively mature medusae. The issues of planktonic dispersion, migration, and spawning are discussed in relation to the life history, behavior and neurobiology of scyphomedusae, with specific examples from recent research on the moon jellyfish, *Aurelia aurita*, and with speculations about other taxonomic groups of Cnidaria.

BEHAVIOURAL RESPONSES TO CONTACT BETWEEN THE SCYPHOZOAN PREDATOR *CYANEA CAPILLATA* AND THE PREY *AURELIA AURITA*. L.J. Hansson, Göteborg University, Kristineberg Marine Research Station, S-45034 Fiskebäckskil, Sweden

The inter-specific relationship between two scyphozoan medusae was studied in the Gullmarsfjorden, Sweden. Experiments were made in the field in order to study the behaviour when the predator *Cyanea capillata* (L.) encounters an individual of the prey *Aurelia aurita* (L.). An underwater video camera, operated by SCUBA divers, was used to record the motility patterns of the medusae.

The observed reaction in *A. aurita* varied when different parts of the medusan body were brought in contact with the marginal tentacles of *C. capillata*. The umbrella margin of *A. aurita* was highly sensitive and in this region of the body, contact with a single tentacle of *C. capillata* was enough to induce a typical change in the motility pattern. However, the nematocysts on the tentacles of *C. capillata* did not have to discharge in order to cause this response in *A. aurita*. The same behavioural change could be evoked by merely mechanical stimuli.

The medusa of *C. capillata* also responded to mechanical stimulation. When a pulling force was applied to the tentacles, a change in both swimming direction and swim pulse frequency were observed. Possible ecological significance of the behaviour is discussed.

SENSORY PHYSIOLOGICAL STUDIES OF THE FIRST ANTENNA OF CALANOID COPEPODS. D.K. Hartline and P.H. Lenz, Békésy Laboratory of Neurobiology, Pacific Biomedical Research Center, University of Hawaii, Honolulu, HI 96822 USA

One of the keys to survival of calanoid copepods is a rapid escape "jump" to sudden mechanical stimuli. Recent electrophysiological studies of sensory cells in the antennae of these animals have demonstrated discharge of giant spikes in response to various mechanical stimuli of setae on the distal tip of the first antennae (Yen et al. *J. Plankton Res.* 14: 495 [1992]; Lenz and Yen *Bull. Marine Sci.* 53: [1993]). In the present studies, extracellular recordings of nerve impulse traffic in response to controlled mechanical stimuli to the antennal tip were made using the methods of Gassie et al. (*Bull. Marine Sci.* 53: 96 [1993]) in calanoids. Abrupt water movements (trapezoidal wave forms), mimicking the type of hydrodynamic signal present in potential predatory lunges, triggered responses in two reidentifiable giant units at water velocities as low as 10 microns/sec. This is comparable to water velocity thresholds reported in calanoids for sinusoidal forms of mechanical stimulus.

In another electrophysiological approach, suction electrode recordings were made from the antennal nerve of *Gaussia princeps* by cutting a small window in the ventral exoskeleton at the base of the antenna. Touching setae on the distal tip elicited impulses picked up by the electrodes. Electrical stimulation through the same electrode elicited a rapid all-or-none abduction of the long anteriorly projecting seta, #8 (Weatherby et al. *J. crust. Biol.* 14: 670 [1994]).

Escape reactions in some calanoid copepods show a high sensitivity to water velocities for vibratory signals of unusually high frequency for a crustacean (1000 Hz; see Herren et al., this volume). The mechanoreceptors described here possess the characteristics needed to be the detectors of the disturbances leading to these escape reactions.

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WATER FLOW EFFECTS ON ZOOPLANKTON ESCAPE BEHAVIORS FROM CORAL PREDATORS. K.B. Heidelberg, K.P. Sebens, and J.E. Purcell, Horn Point Environmental Laboratory, Center for Environmental and Estuarine Studies, The University of Maryland System, PO Box 775, Cambridge, MD 21613, USA

Studies addressing coral predator's effects on zooplankton assemblages have not examined the role of the zooplankton behavior on capture efficiencies. The relationships between capture and escape based on zooplankton behavior, coral tentacle size, and water flow speed were examined for the two scleractinian corals, *Meandrina meandrites* and *Madracis mirabilis*. We used an oscillatory, recirculating laboratory flume at the Discovery Bay Marine Lab in Jamaica. Zooplankton encounters with coral tentacles were filmed with a high magnification, CCD camera using infrared back lighting and low, medium, or high oscillating flow speeds that were comparable to local reef conditions. A wide range of taxa of zooplankton behavior was characterized using frame by frame analysis of the video footage. Prey escape abilities, flow speed, and coral species were all found to play an important role in modifying encounter and capture rates. These results explain why coral coelenteron contents do not correspond to ambient zooplankton assemblages.

BEHAVIORAL RESPONSES OF CALANOID COPEPODS TO QUANTITATIVE MECHANICAL STIMULI. C. Herren*, P.H. Lenz, and D.K. Hartline, Békésy Laboratory of Neurobiology, Pacific Biomedical Research Center, University of Hawaii, Honolulu, HI 96822 USA and *Marine Science Program, University of South Carolina, Columbia, SC, USA

Recent advances in electrophysiological techniques have permitted measurement of physiological responses to controlled mechanical stimuli in calanoid copepods (Yen et al. *J. Plankton Res.* 14: 495 [1992]; Lenz and Yen *Bull. Marine Sci.* 53: [1993]); Gassie et al., *Bull. Marine Sci.* 53: 96 [1993]). We report here results of comparable work on behavioral responses to the same stimuli.

Labidocera madurae were tethered to a fine wire and stimulated by water movements produced by a small piezo-electrically driven sphere positioned near by (Gassie et al. 1993 *loc. cit.*). Escape "jumps" were monitored visually through a dissecting microscope. Abrupt (trapezoidal) water movements of as little as 10 nm completed in 100 microseconds (a symmetrical return movement was delivered 2.5 msec later) were sufficient to elicit responses in sensitive animals.

Response thresholds were measured to a trapezoidally-modulated sine wave stimulus of 10 msec onset, 10 msec constant amplitude and 10 msec offset times, for frequencies from 100 to 2400 Hz. Highest displacement sensitivities were observed around 1000 Hz, with sensitivities falling off gradually at lower frequencies and more precipitously at higher frequencies. The velocity threshold, however, was near 10 microns per second at 1000 Hz, paralleling electrophysiological findings. Best velocity sensitivities are compatible with a single sensory impulse being sufficient to trigger an escape reaction under some conditions.

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HYDRODYNAMICS OF OLFACTORY ANTENNAE. M.A.R. Koehl, University of California, Berkeley, CA 94720-3140, USA

A critical step in the process of olfaction is the arrival of chemical signals from the environment to the surface of a chemosensory structure. Many zooplankton use antennae bearing arrays of microscopic hairs to pick up chemical signals from the surrounding water. The fluid flow field in the immediate vicinity of a sensory hair determines the rates at which molecules are captured, hence the hydrodynamic design of an antenna provides the first step in filtering environmental chemical signals. We have been using physical and mathematical models to identify which aspects of the morphology and motion of antennae are important in determining the flow microenvironment of the sensory hairs they bear.

BEHAVIOUR AND ECOLOGY OF CLADOCERA WITH FOCUS ON THE INFLUENCE OF CHEMICAL SIGNALS IN THEIR ENVIRONMENT. P. Larsson, University of Bergen, 5007 Bergen, Norway

This paper gives an overview of how behaviour, morphology and reproduction in filter feeding Cladocera are mediated by chemical signals from predators, competitors and conspecifics. The Cladocerans are preferred prey for many fishes and invertebrates and they got both increased vigilance and direct behavioural responses to chemicals released by these predators. They seem to discriminate between both the type of predators and their environmental situation, and may react with direct avoidance, aggregations in swarms or diel vertical migration. Their tendency to make swarms and diel vertical migrations seems to be strongly modified by the food conditions. It has not been documented that the search for appropriate food is chemically mediated. Some species have cyclomorphosis with a periodic appearance of helmets and longer spines. It has been demonstrated that at least some of these reactions are chemically induced. Cladocerans combine sexual and asexual reproduction. Their parthenogenetic reproduction is in periods broken by formation of males and sexual resting eggs (ephippia). The change in reproductive mode is regulated by both phenological cues like photoperiod, as well as food concentrations and the intensity of chemical signals from their conspecifics or other cladoceran species. Other lifecycle changes are also reported.

CRYPTIC BIOLUMINESCENCE IN THE MIDWATER ENVIRONMENT. M.I. Latz, Marine Biology Research Division 0202, Scripps Institution of Oceanography, La Jolla, CA 92093, USA

One of the strategies midwater animals have adopted for remaining cryptic to silhouette-scanning predators is luminescent countershading, called counterillumination, in which downward-directed bioluminescence replaces oceanic light that has been reflected or absorbed by the body. Because counterilluminating animals respond directly to their optical environment, an understanding of the control of bioluminescence provides an insight into the visual processing capabilities in systems which are poorly understood. In the penaeid shrimp, *Sergestes similis*, downward-directed illumination detected by the eyes results in light emission from modified portions of the hepatopancreas. Bioluminescence matches the physical characteristics of oceanic light. Experimental results suggest that two physiological control systems, one neural and the other hormonal, regulate the induction and control of counterillumination. One hypothesis is that the induction of bioluminescence is linked to light adaptation of the eye. Ultimately, deciphering the control of light emission in *S. similis* will aid in understanding the ecological roles of bioluminescence and vision in predator-prey interactions and trophic dynamics in the midwater environment.

NEURAL DEVELOPMENT IN THE PLANKTONIC AND EARLY BENTHIC STAGES OF THE PALINURID LOBSTER, *JASUS EDWARDSII*. M.S. Laverack, D.L. Macmillan and S.L. Sandow, Department of Zoology, University of Melbourne, Parkville Vic. 3052 Australia

Jasus edwardsii has a series of eleven phyllosoma stage larvae that are morphologically adapted for a fully planktonic existence. These are followed by a puerulus stage which, although it has the general body form of the adult, is also adapted for swimming, and then by the first of the truly benthic juvenile stages. Using transmission electron microscopy we compared transverse sections of connectives in the ventral nerve cord of the first phyllosoma, the puerulus and the first post-puerulus stage at a number of levels along its length. We found that the anterior cord of the phyllosoma has approximately the same number of neurons as the puerulus. This has implications for our understanding of crustacean larval sensory systems because previous work shows that by far the largest number of fibres in the nerve cord are sensory. Fibre counts in the post-puerulus increase in the expected manner. The cord structure of the puerulus and post-puerulus is the same as that found in the adult whereas that of the phyllosoma is not organised in the same way.

LECTIN BINDING TO SURFACE GLYCOPROTEINS ON COULLANA SPP. (COPEPODA: HARPACTICOIDA) CAN INHIBIT MATE GUARDING. D.J. Lonsdale[1], T.W. Snell[2] and M. Frey[1], [1]Marine Sciences Research Center, State University of New York at Stony Brook, NY 11794-5000, [2]School of Biology, Georgia Tech., Atlanta, GA 30320-0230, USA

We tested the hypothesis that surface glycoproteins found on *Coullana* spp. are important mate-recognition factors. Female copepodites (mostly C V's) of *Coullana canadensis* (Maryland) and *Coullana* sp. (Florida) were treated with 0.1 mg ml^{-1} of four lectins that represent a variety of carbohydrate affinities. The females were then washed and exposed to males. Binding of some lectins significantly reduced the ability of males to recognize potential mates and initiate precopulatory mate guarding. Other lectin treatments had no significant effect on this behavior. These data suggest that surface glycoproteins on female *Coullana* spp. are important mating signals for males in the recognition of conspecifics. Our results also suggest that differences in chemical signals among these sibling species may have evolved.

INVOLUTION, INTIMIDATION, ESCAPE: DEFENSIVE STRATEGIES IN PLANKTONIC COELENTERATES. G.O. Mackie, University of Victoria, Victoria, British Columbia, V8W 2Y2, Canada

Confronted with damaging or potentially harmful stimuli some hydromedusae adopt an armadillo-like strategy, pulling in their appendages and closing the bell at the bottom (involution, or "crumpling"). The response is evoked by sharp contact on exterior surfaces. The entire exumbrellar epithelium is a sensory receptor that conducts signals firing the nerves and muscles involved. In some medusae and siphonophores crumpling is accompanied by dramatic visual displays, for instance the blinding, sheet-like luminescence of *Euphysa* and the astonishing, blanching response of *Hippopodius*. The display serves to emphasize the impressive bulk of these largish, slow-moving forms and is mediated by conducting epithelia. For powerful swimmers, escape provides an obvious solution. A short response latency is essential, and giant axons have evolved as rapid conduction pathways in some ctenophores (*Euplokamis*), siphonophores (*Nanomia*) and hydromedusae (*Aglantha*). Some species are acutely sensitive to vibration as well as to direct contact and have evolved sensory receptors resembling vertebrate hair cells that can detect small mechanical displacements caused by water-borne vibrations.

UNCONVENTIONAL SIGNALLING MECHANISMS IN PELAGIC TUNICATES. G.O. Mackie, University of Victoria, Victoria, British Columbia, V8W 2Y2, Canada

The individual zooids of salps and pyrosomes have well developed central and peripheral nervous systems but so far as is known there are no direct nervous connections between the zooids in these pelagic colonies. This is also true of colonial ascidians and distinguishes the Tunicata as a class from ectoproct bryozoans and cnidarian colonies, where the zooids are usually directly interconnected by nerves. Faced with the challenge of responding to sensory stimuli on a colonial basis and achieving coordinated responses in the absence of a colonial nervous system, tunicate colonies have evolved alternative mechanisms. Didemnid ascidians have reinvented the nervous system in the form of a sensory-motor network of conducting myocytes located in the tunic enveloping the zooids. Botryllids use their colonial blood vessels as signalling pathways. Salps have excitable epithelia that play an essential role in coordinating escape locomotion. Conducting epithelia are also known to occur in doliolids, but their function is unknown. Pyrosomes have hit upon the most brilliant solution of all, using photic signalling to communicate defensive responses within and between colonies.

SENSORY ECOLOGY OF PELAGIC TUNICATES: MORE QUESTIONS THAN ANSWERS. L.P. Madin, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

There is still relatively little known about the natural history of gelatinous animals in the plankton, and their sensory ecology remains largely a matter of surmise, based on limited morphological and behavioral data. A variety of sensory structures, either demonstrated or presumed, have been described in the three major groups of gelatinous plankters. In the pelagic tunicates, these include photoreceptors of varying complexity, and several structures that have been suggested to be mechano- or chemoreceptors. Different kinds of environmental information may be important for different scales of behavior. Feeding and predator avoidance are likely to be affected by near-field stimuli from visual, chemical or mechanical sources, while far-field information such as gravity or gradients of light, temperature, or pressure are likely to cue behavior spanning larger time and space scales, such as vertical or ontogenetic migration, aggregation and reproductive cycles. I will use some examples of feeding behavior, swimming orientation, and vertical migration by thaliaceans and appendicularians to illustrate the kinds of sensory mechanisms that seem likely to exist in these animals, and could be rewarding avenues of research.

ORIENTATION AND TRACKING BY HYPERIID AMPHIPODS. N.J. Marshall and M.F. Land, Sussex Centre for Neuroscience, University of Sussex, Brighton, Sussex BN1 9QG, United Kingdom

Many mesopelagic animals have large eyes which are used in a variety of ways. Very little is known of their natural behaviours, however, because of the difficulties in observing them. Hyperiid amphipods have very large compound eyes and behave well when brought to the surface. Using a tank backlit with IR light and an IR sensitive video camera system, we were able to present the animals with a variety of stimuli and observe their reactions in "dark" conditions. Various species had previously been shown to respond to light and dark bars by swimming away, or occasionally approaching the stimulus (Land, M.F., *J. Mar. Biol Assoc. UK* 72: 41-60 [1992]). In this paper we describe much more striking and predictable behaviour in response to a blue light emitting diode (LED - 475 nm). *Brachyscelus* sp. swarmed around the LED as soon as it was switched on and both *Phrosina semilunta* and *Phronima sedentaria* tracked the LED as it moved. They did this either by tilting the body axis towards the LED, or swimming along with it a few body lengths away. Interestingly the part of the eye used to track the LED was not the dorsal acute zone, present in all species, but a frontal region of slightly elevated acuity in the lower eye (see Land, M.F., *J. Comp. Physiol.* 164: 751-762, [1989]). This is consistent with the idea that the upper eye is for viewing small dark objects against the residual downwelling daylight, whereas the lower eye is concerned with luminescent objects.

OBSERVATIONS ON THE ANATOMY AND BEHAVIOUR OF THE CUBOZOAN *CARYBDEA RASTONI*. G.I. Matsumoto, Flinders University of South Australia, Adelaide, South Australia 5001, Australia

The cubozoan *Carybdea rastoni* occurs throughout the Pacific and is very abundant in areas of South Australia. *C. rastoni* has been observed feeding in the field on mysids and larval fish and on *Artemia* in the laboratory. The medusae occur in swarms and are closely associated with sand patches during the day (but are not capable of attachment like *C. sivickisi*) and move up to the surface at dusk for feeding. The species is dioecious and the males secrete a sperm strand that is picked up by the female. Preliminary observations on colloblasts and the optic system will be presented along with field and laboratory observations on anatomy and behaviour.

PLANKTIVORY IN LARVAL FISHES: ENHANCEMENT OF FORAGING ON ZOOPLANKTON BY ULTRAVIOLET SENSITIVE VISION. F.A. McAlary[1], E.R. Loew[2], and W.N. McFarland[1]. [1]Wrigley Marine Science Center, USC, P.O. Box 398, Avalon, CA 90704, USA, and [2]Department Physiology, VRT, Cornell, Ithaca, NY 14853, USA

Most marine and many fresh water larval fishes are obligate, diurnal, visual planktivores. Survival of larvae depends on finding and capturing food, which is usually presented in a patchy framework, as well as avoiding predators. Mortality of larval fishes therefore can be high because of the uncertainties of finding an adequate supply of food. Successful foraging depends not only on the availability of zooplankton but also the sensory abilities of larval fish to detect their planktivorous prey. Feeding experiments reveal that one day old hatchlings and older larvae are capable of detecting and engulfing zooplankton in UV-A light alone. The basis of this sensory capability is the presence of a class of cone photoreceptors containing a visual pigment that maximally absorbs photons between 350 and 370 nm. We suggest that this short wavelength extension of the visual system increases the chance of capturing prey, and may be widespread, especially amongst, larval fishes.

CHARACTERISTICS OF BROAD SPECTRUM NEURONS IN CRUSTACEAN OLFACTORY MIDBRAIN. D. Mellon, Jr., Department of Biology, Gilmer Hall, University of Virginia, Charlottesville, VA 22901, USA

I have recorded electrical activity from broad-spectrum, multiglomerular neurons in the crayfish olfactory midbrain. Intracellular electrophysiological techniques were used to record responses to odorant stimuli applied to the antennules of isolated, perfused crayfish head preparations. I obtained records from three different classes of midbrain neurons that were identified both by their electrical responses to odorants and by their morphology from biocytin-labeled, sectioned material. All three types responded to a complex mixture of five amino acids as well as to solutions of a commercial fish food. At least one of the classes of neuron also responded to individual amino acids and to sugars. The response properties, as well as the morphologies, of the neurons were unique to each type, consisting in Type I of stimulus-dependent excitatory postsynaptic potentials and superimposed impulse trains, in Type II of stimulus-dependent inhibitory postsynaptic potentials, and in Type III of brief trains of impulses that exhibited frequency and impulse-number maxima to stimulus durations that were nominally above threshold, the responses falling sharply to stimuli above or below this narrow range. All three cell types had extensive, multiglomerular dendritic arbors in the olfactory lobe, but each of their respective branching pattern morphologies was distinctive. Two of the neuronal types had additional dendrite branches in the lateral antennular neuropile and the olfactory-globular tract neuropile. I conclude that these broad-spectrum neurons are part of a parallel olfactory pathway that is separate from the putative quality coding olfactory circuitry by which the crayfish nervous system may discriminate between different odorant stimuli.

THE USE OF NOVEL CHEMO-INDUCTIVE SUBSTRATE RESOLVES FACTORS INVOLVED IN RECRUITMENT OF CORAL LARVAE. A.N.C. Morse and P.T. Raimondi, Marine Biotechnology Center and Center for Coastal Studies, Marine Science Institute, University of California, Santa Barbara, CA 93106, USA

Previous studies from our laboratory reported that planula larvae of the shallow-reef Caribbean coral, *Agaricia humilis*, have a stringent requirement for detection of a specific chemical cue for activation of metamorphosis. The result is rapid, permanent attachment to hard reef substrate and development to the single polyp stage. The chemical morphogen, associated with the cell walls of tropical species of non-geniculate coralline algae (Corallinaceae), has been isolated and partially characterized. Manipulation of the hydrophobic property of this morphogenic compound has facilitated its concentrated adsorption to an inert resin bead matrix that can then be secured to a test surface by embedding in adhesive. This novel chemo-inductive substrate, containing a potent morphogen, has recently been deployed by us in field studies with *A. humilis* larvae to test a number of factors that might influence the types of recruitment patterns exhibited by this coral species on the reefs of Bonaire. These include: availability of morphogen, behavioral response of larvae to orientation of substrate, effect of larval time in the plankton on requirement and stringency of recognition, and effect of depth on activity of the morphogen as well as on post-recruitment predation and survival.

SIGNALS, RECEPTORS, TRANSDUCERS AND GENES CONTROLLING SUBSTRATUM-SPECIFIC METAMORPHOSIS: LARVAL ECOLOGY AND PRACTICAL APPLICATIONS. D.E. Morse and A.N.C. Morse, Marine Biotechnology Center, Marine Science Institute, University of California, Santa Barbara, CA 93106, USA

Planktonic larvae of benthic species from 3 phyla (the coral, *Agaricia*; the mollusc, *Haliotis*; and the polychaete, *Phragmatopoma*) recognize specific signal molecules from the environment that induce substratum-specific settlement and metamorphosis. We have found that recognition of these chemical cues plays a major role in determining the distribution of recruits in the natural environment. In *Haliotis* larvae, these processes are controlled by 2 convergent chemosensory pathways that respond to 2 different classes of chemical signals, each recognized by a distinct receptor. To resolve the relative contributions of chemosensory recognition and other environmental factors that control recruitment of *Agaricia humilis* (induced to metamorphose by glycosaminoglycans associated with cell walls of the recruiting crustose red algae), we are using a morphogen-based chemical "flypaper" containing the purified inducer bound to an artificial substratum. Practical applications of such studies are seen in 2 areas: (1) Use of larval signal molecule control points can increase profitability and yield in aquaculture (as larval settlement is far more sensitive to pollutants than is simple survival, providing State and Federal agencies with new bioassays that are more reliable, less expensive and ecologically more significant than those previously based on mortality. (2) Because the signals, receptors, transducers and genes controlling larval settlement are closely related to those controlling cell function, neuronal activity and development in humans, they may provide the basis for new therapeutic and diagnostic agents for human medicine.

EYE DESIGN, VISION AND INVISIBILITY IN PLANKTONIC INVERTEBRATES. D.-E. Nilsson, Department of Zoology, University of Lund, Helgonavägen 3, S-223 62 Lund, Sweden

Unlike the continuous and extended nature of terrestrial visual environments, the visual world of planktonic animals consists primarily of point objects, either bioluminescent sources contrasting against a dark background or dark silhouettes seen against a bright background of downwelling day-light. The eye designs of planktonic invertebrates reveal a number of unusual specializations exploiting this unique visual environment. Some of the more interesting cases are the large camera eyes of alciopid polychaetes, the tubular eyes of some squid, the scanning eyes of heteropod molluscs and various copepod crustaceans, the parabolic mirror eyes of the ostracod crustacean *Gigantocypris*, and the divided compound eyes of euphausiid and hyperiid crustaceans. Many of these eyes provide large-field general vision, which is useful in bright shallow habitats and suits the detection of bioluminescence at any depth. Other eyes have narrow visual fields specialized for spotting objects against the dim downwelling day-light at considerable depths (down to 700 m). A relation between depth and eye design is particularly evident in some crustaceans such as euphausiids and hyperiid amphipods: the deeper the habitat, the more of the eye is concerned with upward vision. The presence of upward-looking predators is the obvious reason for several types of camouflage to reduce the size or contrast of the body silhouette. General transparency is one such adaptation which even involves a special type of transparent compound eye in several crustacean groups.

SENSORY INPUTS TO THE NEURONS UNDERLYING PREY CAPTURE IN THE PTEROPOD MOLLUSC, *CLIONE LIMACINA*. T.P. Norekian, Department of Zoology, Arizona State University, Tempe, AZ 85287-1501, USA

The predatory pteropod mollusc *Clione limacina* is an extreme feeding specialist which feeds only on shelled pteropods from the genus *Limacina*. Direct contact with *Limacina* initiates a prey capture behavior which consists of an explosive extrusion of buccal cones, specialized structures that are used to catch the prey, and acceleration of swimming with frequent turning and looping around the place where *Limacina* was contacted. A system of neurons which controls different components of prey capture behavior in *Clione* has been identified in the cerebral ganglia. Tactile and chemical stimuli, which initiate feeding behavior in intact animals, produce excitatory inputs to these neurons. Tactile inputs from the anterior part of the head produce strong, phasic activation of the neurons and appear to be of particular importance since only direct mechanical contact with the prey initiates prey capture reactions. However, chemosensory inputs also are believed to be important for chemical recognition of the prey. Pure chemical stimuli without the mechanosensory component (*Limacina* juice was used in these experiments) induce a tonic, prolonged activation of the neurons and appear to be very specific.

CONFIRMATION AND MEASUREMENT OF BIOLUMINESCENCE OF THE PELAGIC SHRIMP, *SERGIA LUCENS*. M. Omori[1], H. Fukami[1], and M.I. Latz[2]. [1]Department of Aquatic Biosciences, Tokyo University of Fisheres, 4-5-7, Konan, Minato-ku, Tokyo 108, Japan, [2]Marine Biology Research Division, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093-0202, USA

This initial study is the first direct confirmation of bioluminescence in *Sergia lucens*. Light emission probably originates from the numerous, more than 160, dermal photophores. Light emission was measured by a photon-counting photomultiplier with a computerized data acquisition system and a TV camera equipped with an image intensifier and VTR. Light emission was directed downward from the ventral surface of the body, and occurred overall as a dim continuous glow. The maximum intensity was measured in female with matured ovaries being 1.09×10^8 quanta/sec. This value was nearly equal to that of downwelling illumination between 250 and 300 m depth of the sea during daytime, suggesting that the bioluminescence may be used in countershading the body. Additional research is needed to confirm whether bioluminescence is involved in swarming behavior of this commercially important species.

SOUND DETECTION BY FISHES. A.N. Popper, Department of Zoology, University of Maryland, College Park, MD 20742, USA

Bioacoustics studies have demonstrated that many species of fish use sound for communication. Sounds are used in a variety of behavioral contexts, and provide long-distance, rapid and directional information in all water conditions.

Sound detection capabilities have been studied behaviorally in about 80 species and fishes can be divided into two groups groups--hearing generalists and hearing specialists. Hearing generalists most often detect sounds from below 50 Hz to about 500 to 800 Hz, while hearing specialists often detect signals from below 50 Hz to over 3,000 Hz. Hearing sensitivity in specialists also exceeds that of generalists. Hearing specialists always have some structures associated with the auditory system that enhance sound detection capabilities. Significantly, specialists are found in many fish taxonomic groups, suggesting that similar specializations have arisen multiple times in fish evolution.

This talk will consider the range of hearing capabilities found among fishes and examine some of the characteristics of the peripheral auditory system that are found in hearing generalists and specialists. [Work supported by ONR, NASA, and NIH]

CHEMICAL BASIS FOR PREY SELECTION IN A PELAGIC CNIDARIAN. J.E. Purcell and P.A.V. Anderson, University Maryland, Horn Point Environmental Laboratory, Cambridge, MD 21613; University Florida, Whitney Laboratory, St. Augustine, FL 32086, USA

Dietary analyses have showed that most siphonophores consume primarily crustacean zooplankton, but that *Physalia physalis*, the Portuguese man of war, consumes mostly fish and fish larvae. Intracellular recordings from nematocyst-containing cells in small pieces of *Physalia* tentacles were used to quantify the electrical responses to chemical stimulation. Aqueous stimuli (seawater control, fish mucus extract, and 10 nM - 1 mM amino acids, nucleosides, monosaccharides) were delivered upstream of the tissue by a 0.1 ml vol HPLC rotary loop injector. Seawater caused no response. The fish mucus extract produced 1-13 depolarizing spikes (20 mV max. amplitude). Only the $<3,000$ MW fraction was stimulatory. The various chemical (≥ 100 nM) caused 1-6 spikes of lower amplitude than the mucus extract. Aspartic amino acid, histidine, and serine together comprised 60% of the amino acids in the fish mucus. We conclude that prey capture in *Physalia* is mediated by chemical stimuli from the prey, which may affect nematocyst discharge. Funded by NSF grant BNS-9011030.

MEMORY FOR FISH KAIROMONE IN *DAPHNIA*. J. Ringelberg and E. van Gool, Department of Aquatic Ecology, University of Amsterdam, Kruislaan 320, 1098 Amsterdam, The Netherlands

A chemical, mediated by visually predating fish, enhances phototactic reactivity to relative changes in light intensity in *Daphnia*. In the epilimnion of Lake Maarsseveen, this kairomone is present when large shoals of juvenile perch (*Perca fluviatilis*) roam the open water zone. At dawn, when relative increases in light intensity are maximum, the sensitizing effect leads to extensive downward movements out of the well-lit predation zone and into the hypolimnion. Although no kairomone is present at this greater depth, an equally strong positively phototactic reaction brings the daphnids back into the epilimnion at dusk. Also, migration continues for some days after the juvenile perch have dispersed into the littoral zone. These observations suggest that the sensitizing effect is preserved for some time. Indeed, experiments revealed that sensitivity gradually diminishes over a period of 4-5 days.

MORPHOLOGY OF WING MECHANORECEPTORS INVOLVED IN THE WING RETRACTION REFLEX OF THE PTEROPOD MOLLUSC *CLIONE LIMACINA*. R.A. Satterlie, M. Lagro, M. Titus, S. Jordan and K. Robertson, Arizona State University, Tempe, AZ 85287-1501, USA

Tactile stimulation of the wings (parapodia) of actively swimming *Clione* results in inhibition of swimming and retraction of the wings. Electrophysiological evidence suggests that wing mechanoreceptors have central cell bodies and wide innervation fields in the ipsilateral wing. Scanning electron microscopy of expanded wings reveal ciliary cone processes arranged in a pattern that is similar to the electrophysiologically-determined innervation fields of wing mechanoreceptors. Transmission electron microscopy suggests that the ciliary cone structures are terminal processes of neuron-like cells. Three-dimensional reconstructions of serially-sectioned terminal processes indicate that cell bodies are not found in the wing epithelium or immediately under the epithelium, further supporting the notion that the wing mechanoreceptors do have central cell bodies.

RECEPTION AND PRODUCTION OF HYDRODYNAMIC STIMULI IN CRAYFISH AND SNAPPING SHRIMP. B. Schmitz, Fakultät für Biologie, Universität Konstanz, Postfach 5560, D-78434 Konstanz, Germany

Each organism moving under water produces hydrodynamic stimuli. Red swamp crayfish (*Procambarus clarkii*), which are predominantly active at night, analyze these water movements to detect and localize predators, prey and conspecifics. During development the behavioral responses towards small swimming fish change from escape or rough stimulus lateralization in juvenile crayfish to accurate orientational responses and prey capture in adults. The sensory bases of these changes are analyzed studying the development of hydrodynamic telson receptors, of their central projections, and the connectivity between these hair sensilla and mechanosensory interneurons in the terminal ganglion. Marine snapping shrimp (e.g. *Alpheus heterochaelis*) are able to produce a loud snap as well as a fast water jet by rapidly closing a specialized snapper claw. The time of claw closure is below 750 microseconds as revealed by high speed video analysis and optoelectrical measurements. The acoustic and hydrodynamic signals, which are used in defense against predators and conspecific intruders, but may also serve to stun prey organisms, are analyzed with respect to amplitude, temporal, spatial and spectral parameters. While auditory receptors are missing in snapping shrimp a large number of hair sensilla, and thus potential hydrodynamic receptors, is revealed by scanning electron microscopy.

SURFACE GLYCOPROTEINS SERVE AS CONTACT MATE RECOGNITION PHEROMONES IN ROTIFERS. T.W. Snell and R. Rico-Martinez, School of Biology, Georgia Tech, Atlanta, GA 30332-0230, USA

Pheromonal regulation of invertebrate reproduction influences several important ecological processes like locating conspecifics, recognizing them as potential mates, and transferring sperm. For common zooplankters like copepods and rotifers, behavioral evidence has suggested the existence of sex pheromones, but none has been isolated and characterized. We describe a 29 kD glycoprotein (gp29) on the surface of females of the marine rotifer *Brachionus plicatilis* that acts as a contact mating pheromone. This glycoprotein is glycosylated with oligosaccharides containing N-acetylglucosamine, mannose, and fucose residues and these oligosaccharides are necessary for male recognition of females. Binding of purified gp29 to male receptors reduced mating attempts by 93%. An antibody to gp29 bound to females, reducing male mating attempts by 86%. When purified gp29 is bound to sepharose beads, it is sufficient to elicit male mating behavior. Comparison of gp29 among *B. plicatilis* populations suggests differentiation at the species level. Lectin binding studies with copepods and cladocerans suggest that there are surface glycoproteins present in these groups that could serve as contact mating pheromones.

EXCITABILITY PROPERTIES OF EPITHELIA AND NEURONS IN *POLYORCHIS* (HYDROZOA): THEIR RELEVANCE TO BEHAVIOR. A.N. Spencer, N. Grigoriev and J. Przysiezniak. University of Alberta and Bamfield Marine Station, Bamfield, BC., VOR1B0, Canada

In this talk I will compare and contrast electrical excitability in epithelia and neurons. The characteristics of the demonstrated properties are a combination of conventional and specialized features. Surprisingly, all tissues in hydromedusae are capable of conducting action potentials. Both epithelial layers, whether they are pure pavement epithelium or epithelio-muscular cells, are excitable. These epithelia are capable of behavioral habituation. Action potentials are initiated by touch and propagate through epithelial sheets at velocities that depend on the firing frequency. Using both extracellular recording from excised tissue and patch-clamp recording of cultured cells it can be shown that the conduction velocity decrease that is seen during repetitive stimulation is calcium dependent.

The firing properties of 3 different neuronal types are very different and are related to their particular functions. For example "O" neurons within the ocellar pathway produce graded, oscillatory action potentials that are modulated by light; "B" neurons, which are smooth muscle motor neurons, produce simple, all-or-none action potentials, and SMNs, which are the motor neurons controlling swimming, have variable duration action potentials. For all these cells we are trying to determine which suites of channel proteins have been selected to produce each characteristic excitability property. Preliminary electrophysiological and molecular results will be discussed.

SENSORY POTENTIAL IN CILIATED ZOOPLANKTON: STRUCTURAL AND BEHAVIORAL ASPECTS OF DIET SELECTION IN ROTIFERS. P.L. Starkweather, Department of Biological Sciences and Limnological Research Center, University of Nevada, Las Vegas, NV 89154, USA

Rotifers exhibit a wide range of feeding behaviors which differ in response to changes in nutritional environment or availability of prey. In particular, many suspension-feeding branchionids modify food collection when they encounter foods of differing size, chemical content or available density. Ploimate predatory species differentiate between conspecific prey of distinct ancestry. These observations point to a substantial array of mechano- and chemosensory modalities, of which most, if not all, are based on ciliary structures of the corona. The various cilia, ciliary bundles and cirri appear to be coordinated through a series of nerves and muscles which permit remarkably complicated behaviors when the animals contact individual food cells. Judging from measurements of near-coronal flows, all cilia and compound cilia (cirri) of the rotifer corona operate in an environment characterized by Reynolds Numbers (Re) between 10^{-5} and 10^{-3}. All remote or "contact" sensory reception and resulting behavioral responses are therefore constrained to occur in laminar, viscous fluid flows.

FIELD AND LABORATORY OBSERVATIONS OF THE CUBOZOAN *TRIPEDALIA CYSTOPHORA*: IMPLICATIONS REGARDING VISION. S.E. Stewart, The University of Texas Marine Science Institute, Port Aransas, TX 78373, USA

The adult medusa *Tripedalia cystophora* is small (~1.0 cm bell height) and occupies a coastal mangrove habitat in southwestern Puerto Rico. Like other members of the Class Cubozoa, *T. cystophora* possesses multiple complex eyes as well as pigment-cup ocelli. Field observations indicate no apparent role for the complex eyes in locating mates, other conspecifics or prey. Laboratory experiments confirm a positive phototaxis, but no chemotaxis with regard to prey swarms (cyclopoid copepods of Genus *Oithona*). Research in progress as of August 1994 concerns the possibility of a feeding or other role of the complex eyes in the bell interior, for the complex eyes are oriented inward and have a structure conducive to vision within a 1 cm range. The presentation will cover aspects of the entire study.

INFORMATION, INFORMATION, INFORMATION! SEEING VON UEXKÜLL'S "UMWELT" OF PLANKTONIC CRUSTACEANS AND THE ANIMAL'S REACTIONS TOWARDS IT. J.R. Strickler, University of Wisconsin, Milwaukee, WI 53204, USA

Planktonic crustaceans live within a fluid environment at spatial and temporal scales unfamiliar to humans. For the past 25 years I tried to elucidate the "Umwelt" of these animals using non-intrusive optical techniques. The requirements for choosing a specific optical pathway were stringent: high temporal (msec) and spatial (μm) resolutions, large dynamic ranges (msec to hours, μm to 10 cm), visualization of differences in optical density, three-dimensional observations, and all in the largest vessel possible.

In a video I will show and explain a series of techniques, novel and old ones, addressing some of the following questions: Are algae touched by the setae of the catching animal? Do prey change their swimming pattern in the presence of predators? How large is the encounter radius of a predator? How do animals react to bioturbulence? Can planktonic crustaceans perceive spatial changes in density, viscosity, salinity, and temperature of their surround water?

THE DELAY OF METAMORPHOSIS IN DECAPOD LARVAE DUE TO SUBSTRATE AND CONSPECIFIC CUES. I. Walter and K. Anger, Biologische Anstalt Helgoland, 27493 Helgoland, Germany

Benthic decapods often still possess considerable mobility after metamorphosis. Nevertheless, selection of an appropriate habitat for benthic life by the planktonic larva before metamorphosis might be of advantage, especially if a species is restricted to a very specific habitat. In this study, three decapod species were tested for their ability to delay metamorphosis in the presence or absence of cues from the substrate or from adult conspecifics as "markers" for an appropriate habitat. *Chasmagnathus granulata* and *Sesarma curacaoense* are restricted to specific habitats (muddy substrates of salt marshes and lagoons, and mangrove swamps respectively.

In the laboratory, megalopae of these species performed metamorphosis significantly earlier in the rpesence of adult females than without substrate or conspecifics. *C. granulata* megalopae reacted in the same way to the presence of mud and sand. The marine speider crab *Hyas araneus* is less specific but shows a slight preference for filamentous algal substrates. Megalopae of this species went through metamorphosis signficantly earlier when red algae were offered as a substrate. In all cases, the cues are likely to be chemical as artificial substrates of equal particle size and texture had no effect on the duration of the megalopa stage as compared to control groups with no substrate. Our experiments also indicated that the megalopae of different species may be responsive to habitat cues at different times during their development.

MORPHOLOGICAL STUDIES OF MECHANO- AND CHEMORECEPTIVE SETAE IN THE FIRST ANTENNA OF A CALANOID COPEPOD. T. Weatherby and P.H. Lenz, Biological Electron Microscope Facility and Békésy Laboratory of Neurobiology, Pacific Biomedical Research Center, University of Hawaii, Honolulu, HI 96822 USA

The first antennae of calanoid copepods bear mechanoreceptive setae on their distal tips which physiologically and behaviorally demonstrate exceptional performance characteristics compared to mechanoreceptors in benthic crustaceans (Yen et al. J. Plankton Res. 14: 495 [1992]; Herren, Lenz, and Hartline, this volume). In addition, the first antennae bear at least three types of receptors. We made an ultrastructural TEM study of these receptors.

The long spiniform setae of the distal tip (which presumably give rise to the giant axons reported by Yen *et al.* 1992 *loc. cit.*) show ultrastructural characteristics of pure mechanoreceptors, being characterized by an exceptional number and density of dense-core microtubules (up to 2000 per sensory dendrite). The spiniform setae located along the antennal shaft possess two mechanoreceptors each, and in addition, two chemoreceptors, thin dendrites of which project well into the setal shaft. The setae readily stain with methylene blue, and this dye travels in time into the putative chemosensory somata located near the bases of the setae. These setae, unlike the pure mechanoreceptive setae of the distal tip, possess terminal pores which appear to give access to the external medium. Their characteristics are compatible with their subserving a gustatory function (contact chemo + mechano). Asthetascs along the antennal shaft are characterzed by thin cuticular walls and many fine dendrites with small numbers of microtubules in each. These setae readily stain with azocarmine, but the dye does not readily penetrate to the cell bodies.

Supported by NSF OCE 89-18019 and a grant from the UH President's Development Fund.

RECORDING AND ANALYSIS OF THE TURBULENT PROPULSION JET OF EUPHAUSIID SHRIMP (CRUSTACEA). K. Wiese, Zoologisches Institut und Zoologisches Museum der Universität, Martin Luther King Platz 3, 20146 Hamburg, Germany

The notion that turbulent flow generated by swimming shrimp constitutes a signal used generally in intraspecies communication and in recruitment to schools and in control of formation swimming in euphausiids has been tested in tetheredly swimming *Euphausia superba*, *Meganyctiphanes norvegica*, and *Leander adspersus*. Recording of the propulsion jet was first done by pressure sensitive microphone, later using hot wire anemometry. Detailed FFT spectra of the signals obtained show a base frequency specific for the species of shrimp together with 2-4 harmonics at multiples of base frequency. Broadband background noise as revealed by analysis of a signal obtained by identical recording technique from turbulent flow generated by a model ship propeller, shows strong contribution to the spectrum at low frequencies, weak contribution at high frequencies, is absent in the turbulent flow signals produced by the measured swimming shrimp. The flow sensor within the antennules of *Euphausia*, a proprioceptive scolopal organ controlling movement in the basal hinge of the ventrally directed flagella, matches all requirements connected with reception of flow velocity, flow direction and analysis of spectral content of the turbulent flow signal.

NATURAL INGESTION RATES OF MARINE CALANOID COPEPODS IN WATERS

NATURAL INGESTION RATES OF MARINE CALANOID COPEPODS IN WATERS AROUND THE NANSHA ISLANDS OF THE SOUTH CHINA SEA. C.K. Wong[1], Q.C. Chen[2], and L.M. Huang[2], [1]Department of Biology, The Chinese University of Hong Kong, Shatin, Hong Kong, and [2]South China Sea Institute of Oceanology, Guangzhou, The People's Republic of China

The gut fluorescence technique was used to estimate the grazing rate of calanoid copepods in tropical waters around the Nansha Islands of the South China Sea. Chlorophyll *a* concentrations within the upper 100 m of the water column ranged from 0.19 to 1.0 mg m^{-3}. Numerically dominant calanoid copepod species in the study area included *Acartia erythraea, Undinula vulgaris* and *Rhincalanus cornutus*. Gut pigment contents were measured for eighteen species. Ingestion rates were determined from measurements of gut pigment content and gut evacuation rate. Pronounced diel and spatial variations in ingestion rate were observed in some species. In species with sufficient data for comparison, ingestion rates were usually higher during the night and evening than during the day. Average ingestion rate for calanoid copepods was 202.6 ng Chl *a* $animal^{-1}$ day^{-1}. Community grazing rate, estimated from average ingestion rate and average copepod abundance, showed that $<0.5\%$ of total chlorophyll *a* standing stock was grazed by calanoid copepods each day.

MATE TRACKING IN COPEPODS: PHEROMONES OR SPECIES-SPECIFIC WAKES? J. Yen, S. Colin, M. Doall, P. Moore[1], A. Okubo, and J.R. Strickler[2], Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000, USA; [1]Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403, USA; [2]Center for Great Lakes Studies, University of Wisconsin, Milwaukee, WI 53208, USA

An important behavioral response of copepods (in addition to prey capture and predator avoidance) is mating. Here we present three dimensional tracking of paths taken by the pelagic marine copepod, *Temora longicornis*, while seeking and grabbing mates in the dark. The track of the male precisely follows the track of the female, initiated at distances greater than 20 body lengths apart and separated by times of more than 5 sec. Through analyses of the strength of the signal generated by the female vs. the signal strength at the point when the male crosses her path, we wish to ascertain the potential importance of the fluid mechanical vs. chemical cue as a trigger of mating behavior.

CHEMOSENSORY ECOLOGY OF MARINE LARVAE: BENTHIC-PELAGIC COUPLING. R.K. Zimmer-Faust, University of South Carolina, Columbia, SC 29208, USA

Habitat colonization by planktonic larvae is a dominant factor controlling population dynamics of most benthic invertebrates. Chemical properties of marine environments are important cues used by larvae to select settlement sites. To a large extent, studies on settlement have been limited by a lack of technology for rapidly assessing larval behavior. We have overcome this difficulty by applying computer-video motion analysis to non-invasively track the paths made by free-swimming planktonic larvae. Our results indicate chemically-mediated changes in swimming behavior demonstrating a clear association between application of a dissolved chemical stimulus and rapid behavioral response by oyster larvae. Behavioral responses differ for metabolites released by adult conspecifics and exudates released by microalgal prey. Chemoreceptive behavior suggestive of larval settlement is therefore not a general response evoked by all novel organic compounds. Our field and laboratory findings are consistent in identifying low molecular weight peptides with arginine at the C-terminal as the natural, water-soluble cues inducing oyster settlement. Cue production may be linked to general metabolic processing or to digestion of protein acquired by benthic heterotrophs through dietary sources. Remarkably, in estuarine environments, such conditions are most commonly met by the aggregations of postmetamorphic oysters and their associated communities on oyster reefs.

PARTICIPANT LIST

Dr. Julie W. Ambler, Department of Biology, Millersville University, P.O. Box 1002, Millersville, PA 17551, USA
jw_ambler@ daffy.millersv.edu

Dr. Jelle Atema, Boston University Marine Program, Marine Biological Laboratory, Woods Hole, MA 02543, USA

Dr. Steve Bollens, Biology Department, Woods Hole Oceanographic Institute, Woods Hole, MA 02543, USA
bollens@cole.whoi.edu

Dr. Geoff Boxshall, The Natural History Museum, Cromwell Road, London SW7 5BD, UK
g.boxshall@nhm.ic.ac.uk

Mr. Matthew Brewer, University of Wisconsin, 446 Birge Hall, 430 Lincoln Dr., Madison, WI 53706, USA
mbrewer@macc.wisc.edu

Dr. Howard I. Browman, Maurice-Lamontagne Institute, Fisheries and Oceans Canada, P.O. Box 1000, Mont-Joli, Quebec, Canada G5H 3Z4,
h_browman@imll.iml.dfo.ca

Dr. Theodore H. Bullock, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, USA
tbullock@ucsd.bitnet

Dr. Edward J. Buskey, Marine Science Institute, The University of Texas at Austin, Port Aransas, TX 78373-1267, USA
buskey@utmsi.zo.utexas.edu

Dr. James Case, Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA 93106, USA
case@omni.ucsb.edu

Dr. John Arnold, Pacific Biomedical Research Center, University of Hawaii, Honolulu, HI 96822, USA

Mr. Alexander B. Bochdansky, Ocean Science Centre, Memorial University of Newfoundland, St. John's, Newfoundland, A1C 5S7, Canada
bochdan@morgan.ucs.mun.ca

Dr. Horst Bleckmann, Zoologisches Institut der Universität Bonn, Poppelsdorfer Schloβ, D-53115 Bonn, Germany

Dr. Thomas Breithaupt, Fakultät für Biologie. Universität Konstanz, Postfach 5560 (M618), D-78434 Konstanz, Germany
thomas.breithaupt@uni.konstanz.de

Dr. Harold Bright, Molecular, Cell and Environmental Biology, Office of Naval Research, Ballston Tower One, 800 N. Quincy St., Arlington, VA 22217-5660

Dr. Bernd-Ulrich Budelmann, Marine Biomedical Institute, University of Texas Medical Branch, Galveston, TX 77555-0863, USA
budelmann@mbian.utmb.edu

Dr. Marie H. Bundy, Great Lakes Environmental Research Laboratory, NOAA, 2205 Commonwealth Blvd., Ann Arbor, MI 48105, USA
bundy@glerl.noaa.gov

Dr. Nancy M. Butler, Flathead Lake Biological Station, The University of Montana, 311 Biostation Lane, Polson, MT 59860, USA
nbutler@selway.umt.edu

Dr. Jack H. Costello, Department of Biology, Providence College, Providence, RI 02918-0001, USA
costello@providence.edu

Dr. Thomas W. Cronin, Department of Biological Sciences, University of Maryland Baltimore County, 5401 Wilkens Ave., Baltimore, MD 21228-5398, USA
cronin@umbc7.umbc.edu

Dr. Don Deibel, Ocean Science Centre, Memorial University, St. John's, Newfoundland, A1C 5S7, Canada
ddeibel@kean.ucs.mun.ca

Ms. Lisa Dilling, Department of Biological Sciences, University of California, Santa Barbara, CA 93106, USA
dilling@lifesci.lscf.ucsb.edu

Dr. Stanley I. Dodson, Department of Zoology, University of Wisconsin, 117 West Johnson Street, Madison, WI 53706, USA
dodsons@macc.wisc.edu

Dr. Lynda Farley, Boston University Marine Program, Woods Hole, MA 02543, USA
farley@biology.bu.edu

Dr. Richard Forward, Jr., Duke University Marine Laboratory, Beaufort, NC 28516-9721,
rforward@acpub.duke.edu

Dr. Tammy Frank, Harbor Branch Oceanographic Institution, 5600 U.S. 1 North, Fort Pierce, FL 34946, USA
harbofra@class.org

Dr. Charles Galt, Biology Department, California State University, Long Beach, CA 90840-3702, USA
galt@csulb.edu

Mr. Erik van Gool, Department of Aquatic Ecology, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, The Netherlands

Dr. Jack Davidson, Sea Grant College Program, School of ocean and Earth Science and Technology, University of Hawaii, 1000 Pope Road, Honolulu, HI 96822, USA

Dr. Luc De Meester, Universiteit Gent, Laboratory of Animal Ecology, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium
Luc.DeMeeste@rug.ac.be

Mr. Michael Doall, Marine Science Research Center, State University of New York at Stony Brook, Stony Brook, NY 11794-5000, USA

Dr. Tone Falkenhaug, University of Tromsø, The Norwegian College of Fishery Science, 9037 Tromsø, Norway
tonef@nfh.uit.no

Dave Featherstone, Békésy Laboratory of Neurobiology, P.B.R.C., University of Hawaii, 1993 East-West Road, Honolulu, HI 96822-2359, USA
davef@wana.pbrc.hawaii.edu

David M. Fields, State University of New York, Stony Brook, c/oNELH, P.O. Box 1749, Kailua-Kona, HI 96745, USA
fields@uhunix.uhcc.hawaii.edu

Ms. Melissa Frey, Marine Sciences Research Center, State University of New York at Stony Brook, NY 11794-5000, USA

Ms. Jasmine Gokcen, Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, USA
gokc0001@gold.tc.umn.edu

Dr. Wulf Greve, Biologische Anstalt Helgoland, Zentrale Hamburg, Notkestraβ 31, 22607 Hamburg, Germany

Dr. Michael Hadfield, Kewalo Marine Laboratory, P.B.R.C., University of Hawaii, Honolulu, HI 96822, USA. hadfield@uhunix.uhcc.hawaii.edu

Dr. William M. Hamner, Department of Biology, University of California at Los Angeles, Los Angeles, CA 90024-1606, USA
hamner@biology.lifesci.ucla.edu

Dr. Daniel K. Hartline, Békésy Laboratory of Neurobiology, P.B.R.C., University of Hawaii, 1993 East-West Road, Honolulu, HI 96822-2359, USA
danh@uhunix.uhcc.hawaii.edu

Ms. Christen Herren, Department of Biology, University of South Carolina, Columbia, SC 29208, USA

Dr. Petter Larsson, Museum of Zoology, University of Bergen, Muséplass 3, N-5007 Bergen, Norway
petla@oscar.bbb.no

Dr. Petra H. Lenz, Békésy Laboratory of Neurobiology, P.B.R.C., University of Hawaii, 1993 East-West Road, Honolulu, HI 96822-2359, USA
petra@wana.pbrc.hawaii.edu

Dr. George O. Mackie, Department of Biology, University of Victoria, Victoria, BC, V8W 2Y2, Canada
mack@uvvm.uvic.ca

Dr. Laurence P. Madin, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA lmadin@cliff.whoi.edu

Dr. George Matsumoto, Flinders University of South Australia, Department of Biological Sciences, GPO Box 2100, Adelaide, South Australia, 5001, Australia
bigim@cc.flinders.edu.au

Ms. Peggy Hamner, Department of Biology, University of California at Los Angeles, Los Angeles, CA 90024-1606, USA
hamner@biology.lifesci.ucla.edu

Mr. Lars J. Hansson, Göteborgs Universitet, Marina forskiningstationen vid, Kristineberg, S-450 34 Fiskebäckskil, Sweden

Ms. Karla B. Heidelberg, Horn Point Environmental Laboratory, University of Maryland, Box 775, Cambridge, MD 21613, USA
karla_b_heidelberg@umail.umd.edu

Dr. Mimi A.R. Koehl, Department of Integrative Biology, University of California at Berkeley, Berkeley, CA 94720, USA
cnidaria@violet.berkeley.edu

Dr. Michael I. Latz, Marine Biology Research Division 0202, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, USA
mlatz@uscd.edu

Dr. Darcy J. Lonsdale, Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000, USA
dlonsdale@ccmail.sunysb.edu

Dr. David L. Macmillan, Department of Zoology, University of Melbourne, Parkville, Victoria, 3052 Australia
zoomac@ariel.ucs.unimelb.edu.au

Dr. N. Justin Marshall, Sussex Centre for Neuroscience, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK

Dr. Florence McAlary, Wrigley Marine Science Center, University of Southern California, P.O. Box 398, Avalon, CA 90704, USA

Dr. William McFarland, Wrigley Marine Science Center, University of Southern California, Avalon, CA 90704, USA

Dr. Aileen N. C. Morse, Marine Biotechnology Center, Marine Science Institute, University of California, Santa Barbara, CA 93106, USA
a_morse@lifesci.lscf.ucsb.edu

Dr. Tigran Norekian, Department of Zoology, Arizona State University, Tempe, AZ 85287-1501, USA
attpn@asuvm.inre.asu.edu

Prof. Makoto Omori, Department of Aquatic Biosciences, Tokyo University of Fisheres, 4-5-7, Konan, Minato-ku, Tokyo 108, Japan
makomori@tokyo-u-fish.ac.jp

Dr. Jenny E. Purcell, Horn Point Environmental Labs, University of Maryland, P.O. Box 775, Cambridge, MD 21613, USA
purcell@hpel.umd.edu

Dr. Richard Satterlie, Department of Zoology, Arizona State University, Tempe, AZ 85287, USA
aaras@asuvm.inre.asu.edu

Dr. Kenneth P. Sebens, Department of Zoology, University of Maryland, College Park, MD 20742, USA
KS95@umail.umd.edu

Dr. Andrew Spencer, Bamfield Marine Station, Bamfield, BC., VOR1B0, Canada
andrew.spencer@ualberta.ca

Dr. Peter L. Starkweather, Department of Biological Science, University of Nevada, 4505 Maryland Parkway, Las Vegas, NV 89154, USA
peters@nevada.edu

Dr. DeForest Mellon, Jr., Department of Biology, Gilmer Hall, University of Virginia, Charlottesville, VA 22903, USA DM6D@virginia.edu

Dr. Dan E. Morse, Marine Science Institute, University of California, Santa Barbara, CA 93106-6150, USA
d_morse@lifesci.lscf.ucsb.edu

Dr. Dan-E. Nilsson, Department of Zoology, University of Lund, Helgonavägen 3 , S-223 62 Lund, Sweden
zdan@gemini.ldc.lu.se

Dr. Arthur N. Popper, Department of Biology, University of Maryland, College Park, MD 20742, USA
ap17@umail.umd.edu

Dr. Joop Ringelberg, Universisteit van Amsterdam, Sectie Aquatische, Oecologie/Oecotoxicologie, Kruislaan 320, 1098 SM Amsterdam, The Netherlands admiraal@bio.uva.nl

Dr. Barbara Schmitz, Fachbereich Biologie, Universität Konstanz, Postfach 5560 (M618), D-78434 Konstanz, Germany
bimarkl@nyx.uni-konstanz.de

Dr. Terry W. Snell, School of Biology, Georgia Institute of Technology, Atlanta GA 30332-0230, USA
terry.snell@biology.gatech.edu

Dr. Ole B. Stabell, University of Trømsø, The Norwegian College of Fishery Science, 9037 Tromsø, Norway
oles@nfh.uit.no

Dr. Deborah K. Steinberg, Institute of Marine Sciences, University of California, Santa Cruz, CA 95064, USA
steinber@biology.ucsc.edu

Mr. Scott Stewart, Marine Science Institute, The University of Texas at Austin, P.O. Box 1267, Port Aransas, TX 78373-1267, USA
stewart@utmsi.zo.utexas.edu

Ms. Cynthia Suchman, Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA
csuchman@gsosun1.gso.uri.edu

Ms. Ismeni Walter, Meeresstation, Meeresökologisches Labor., 24783 Helgoland, Germany

Dr. Konrad Wiese, Universität Hamburg, Zoologisches Institut und Museum, Martin-Luther-King-Platz 3, 20146 Hamburg 13, Germany

Dr. Jeannette Yen, Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000, USA
jyen@ccmail.sunysb.edu

Dr. J. Rudi Strickler, Center for Great Lakes Studies, University of Wisconsin, 600 E. Greenfield Avenue, Milwaukee, WI 53204-2944, USA

Dr. Barbara Sullivan, Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA
bsull@gsosun1.gso.uri.edu

Ms. Tina M. Weatherby, Biological Electron Microscope Facility, Pacific Biomedical Research Center, University of Hawaii, 1993 East-West Road, Honolulu, HI 96822, USA
tina@wana.pbrc.hawaii.edu

Dr. C. Kim Wong, Biology, The Chinese University of Hong Kong, Shatin, NT, Hong Kong
b164762@hp720a.csc.cuhk.hk

Dr. Richard K. Zimmer-Faust, University of South Carolina, Department of Biological Sciences, Columbia, SC 29208, USA
dick@tbone.biol.scarolina.edu

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