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A SYMPOSIUM ON CHEMICAL FACTORS THAT INFLUENCE THE SETTLEMENT AND METAMORPHOSIS OF MARINE INVERTEBRATE LARVAE: INTRODUCTION AND PERSPECTIVE

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The distribution and abundance of benthic marine invertebrates can ultimately be traced to patterns of larval settlement and metamorphosis. While interactions of adult organisms with one another and with their environment have received considerable attention by marine ecologists in the past, particularly the roles of competition, predation and disturbance (Dayton, 1971; Menge, 1976), the significance of settlement and recruitment processes, long recognized as important (Mortensen, 1921; Day and Wilson, 1934; Thorson, 1946), has only recently been highlighted (Connell, 1985; Gaines and Roughgarden, 1985). Although the passive transport and deposition of larvae may be important in determining the patterns of species distribution on the sea bottom, particularly at larger spatial scales (Butman, 1987), studies in both the laboratory and field have provided extensive evidence for an active role by larvae in substrate selection at the time of settlement (Crisp, 1974; Strathmann and Branscomb, 1979; Watanabe, 1984; Butman et al., 1988; Raimondi, 1988).

Most benthic marine invertebrates produce pelagic larvae that spend hours to months in the plankton before settling and metamorphosing into their adult forms. Until a few decades ago, it was generally believed that larvae settle on a rigid schedule and in a random fashion, with the distribution of adults contingent on post-settlement survival (Nelson, 1928; Colman, 1933). Subsequently, extensive evidence has accumulated that larvae of many species can prolong their planktic existence and exercise substrate selectivity. Larval settlement and metamorphosis are now largely regarded as responses to complex and often highly specific environmental stimuli (reviews in Crisp, 1974; 1984; Chia and Rice, 1978; Burke, 1983; Hadfield, 1986). Studies have demonstrated behavioral responses of larvae to several physical factors, including light, gravity, and fluid velocity (Crisp, 1955; Thorson, 1964; Wethey, 1986), but, by and large, the most influential cues appear to emanate from biological sources, and these appear to be chemical in nature. Chemical cues have been implicated in the settlement and metamorphosis of a wide variety of species, in particular, those that form conspecific aggregations (reviewed by Burke, 1986), those that settle on or near a source of food (Hadfield, 1978; Switzer-Dunlap, 1978; Morse and Morse, 1984; Hadfield and Scheuer, 1985; Chia and Koss, 1988), and those that settle on films of microorganisms (Wilson, 1955; Brancato and Woollacott, 1982; Kirchman et al., 1982; Maki and Mitchell, 1985). Also described is the avoidance of substrata by larvae because of the presence of competitor or predatory species (Young and Chia, 1981; Standing et al., 1984; Woodin, 1985). Understanding the factors that initiate invertebrate larval settlement is particularly important in two areas of human endeavor, artificial cultivation of marine invertebrates (aquaculture or mariculture), and the prevention of biofouling. Many commercially important invertebrate species have planktic larvae that settle and metamorphose in response to unknown chemical cues. The feasibility of aquaculture for many of these species is dependent not only on the growth of the adults, but also on the settlement success of their larvae.

Biofouling, the colonization of manmade structures by marine organisms, is a subject of great concern, primarily in the shipping industry (see papers in Costlow and Tipper, 1984). The primary fouling invertebrates settle and metamorphose gregariously after perceiving chemical signals associated with microbial films or adjacent conspecific adults. Knowledge of the chemical processes that lead to the settlement of model invertebrate species is the first step toward understanding, and ultimately controlling, the settlement of commercially important species. In addition, such knowledge could be of considerable importance in addressing the impact of humans on the marine benthos, particularly the use and disposal of toxic paints, heavy metals, detergents and solvents.

Interest in the biology of marine invertebrate larvae has prompted several symposia and workshops; most recent have been "Factors Causing Recruitment of Larvae from the Plankton," held in conjunction with the International Symposium on Marine Plankton, in Shimizu, Japan, 1984 (Montgomery, 1985), and the "Larval Biology Workshop," held at Friday Harbor Laboratories, University of Washington, 1985 (Cameron, 1986). While primary interest at these symposia was focused on ecological aspects of larval development and larval life history patterns, chemical factors affecting invertebrate larval settlement and metamorphosis were discussed in some detail, and a reading of the appropriate papers (see *Bulletin of Marine Science,* 37(2), 1985, 4 titles, and 39(2), 1986, 7 titles) would form a useful introduction to the work and discussions presented here.

A symposium entitled "Chemical Factors that Influence the Settlement and Metamorphosis of Marine Invertebrate Larvae" was held in San Francisco at the 1988 Annual Meeting of the American Society of Zoologists. Six speakers gave 30-minute presentations on the afternoon of 27 December, and an additional seven speakers presented contributed papers on the morning of 28 December. The presentations and resultant papers published here and in the 1988 abstracts of *American Zoologist* (vol. 28(4)) provide provocative new data and conjecture on a wide variety of topics relevant to the symposium title. They include both general and specific metamorphic inducers, inhibitors of metamorphosis, mechanisms of induction at the larval surface, and mechanisms of internal activation of metamorphic morphogenesis. Some papers also add insight into distinctions between inducers of settlement and of metamorphosis. Data on 14 species in several phyla were contributed in these talks, increasing understanding of both the diversity and similarities of settlement and metamorphic induction processes across a spectrum of marine invertebrates.

Understanding of the role of generalized, soluble, environmental chemicals in initiating settlement behavior in invertebrate larvae has been considerably advanced. Bonar et al. (1990) and Coon et al. (1988) have exposed the role of ammonia in triggering settlement behavior in oyster larvae. It is clear that such settlement is prerequisite for larvae to arrive in benthic settings where metamorphosis itself can be elicited. These authors conjecture that settlement behavior in oyster larvae results from non-specific cellular responses to the relatively high external ammonia concentrations that a larva might encounter on being carried by currents into a dense assemblage of adult oysters where surface-bound factors probably stimulate metamorphosis. C. Cuomo, in a symposium talk not published here, introduced the useful concept that inorganic compounds produced by biogeochemical processes (e.g., H_2S) might promote passive descent of larvae from the water column through non-specific "shock" or narcotizing effects.

The list of invertebrate species whose larvae metamorphose in response to elevated concentrations of potassium is rapidly growing. Stricker (1988) added an additional phylum by demonstrating that bryozoan larvae metamorphose when potassium ion is elevated by 10 mM. Potassium-induced metamorphosis provides a useful non-specific test for metamorphic competence, something long needed in many studies of metamorphic induction of marine invertebrate larvae (Baloun and Morse, 1984). Pennington and Hadfield (1988; 1989) provide another competence test, a series of alcohols and solvents that induce metamorphosis in at least two gastropod species. These substances may prove useful for other species, but perhaps more importantly, workers should be warned that unless totally removed from their extraction products, solvents might give false positive results in induction bioassays.

The paper by Maki et al. (1990) summarizes interesting new data on the selectivity of competent barnacle larvae for both species and density of bacteria in marine surface films. These authors also demonstrated that responses of barnacle larvae to bacterial films vary with both larval age and age of the bacterial film, the latter probably being a reflection of heterogeneity in bacterial exopolymers, principally peptides. Similar complexities may define for many invertebrates the criteria for metamorphosis in response to generalized surface characteristics as opposed to the species-specific recognitions of others. Metamorphic stimulation of oyster larvae may be a good example (Bonar et al., 1990).

Naturally occurring inhibitors of metamorphosis have received little attention. Davis and Wright (1988) reported that compounds associated with the tunics of certain ascidians deter settlement by invertebrate larvae. In contrast, the chronic effects of environmental pollutants on development of abalone larvae were less severe than one might have predicted based on short-term toxicity testing (Hunt and Anderson, 1988). Metamorphosis of abalone larvae declined significantly during chronic exposure to zinc at concentrations in excess of 19 μg/liter, a level that realistically could be experienced in municipally polluted areas. The potential for chemical perturbation in the marine environment to either inhibit larval settlement or induce it inappropriately remains largely unexplored.

The chemical nature of inducers of settlement and metamorphosis, as well as their modes of action on specific larvae, have been clarified by the studies described in the papers (included here) by Morse and by Barlow on abalones, by Hadfield and Pennington on the nudibranch mollusc *Phestilla sibogae,* by Bonar et al. on oysters, and by Pawlik on the polychaete *Phragmatopoma lapidosa californica.* Morse also discusses recent work in his laboratory on corals and on *P. (lapidosa) californica.* While significant details have been uncovered for each species, broad cross-species generalizations have yet to be realized, and there is some disagreement among workers on the nature and mode of action of inducers. This is not unexpected in a relatively new and dynamic field, and new revelations are anticipated as the methods of biochemistry, molecular biology, electrophysiology, and genetics come into greater use in the exploration of chemical factors that influence the settlement and metamorphosis of marine invertebrate larvae.

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