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# Chapter 6
# Induction of Marine Invertebrate Larval Settlement: Evidence for Chemical Cues

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The invertebrates of the marine benthos include representatives of all the major phyla of animals, and some, such as the echinoderms, live exclusively in this domain. Approximately 80% of marine invertebrates, or roughly 90,000 species, produce microscopic larvae that develop in the plankton (Thorson 1964). These larvae, which have morphologies and diets completely unlike those of their parents, may drift great distances before contacting a suitable substratum and metamorphosing into their adult form. In this chapter, I review evidence for environmental chemical signals that initiate the transition from planktonic larva to benthic adult. The information presented here is largely excerpted from a review of the chemical ecology of marine invertebrate settlement (Pawlik 1992). It is presented in this volume for the sake of completeness and to benefit readers who might otherwise not encounter it in the literature on marine biology.

Until the latter half of this century, the predominant opinion held by marine biologists was that invertebrate larvae metamorphosed in the water column and sank to the bottom, having little ability to affect their distribution; hence, the site of settlement was randomly determined (e.g., Petersen 1913; Colman 1933). This view gave way as considerable evidence accumulated that larvae respond to various physical and biological factors, and, moreover, they delay settlement until a

suitable substratum is contacted (reviewed in Thorson 1966; Meadows and Campbell 1972; Scheltema 1974; Burke 1983; Crisp 1984). More recently, the processes that control the recruitment of invertebrate larvae have sparked considerable interest among ecologists (Connell 1985; Gaines and Roughgarden 1985; Sutherland 1990; Menge 1991), with some concomitant debate over the importance of active substratum selection versus passive deposition in determining subsequent patterns of abundance (reviewed in Butman 1987). There is ample experimental evidence, however, that differential larval settlement largely predicts patterns of benthic recruitment, particularly on hard substrata (R. R. Strathmann et al. 1981; Keough 1983; Watanabe 1984; Bushek 1988; Raimondi 1991); and active substratum selection has been demonstrated in laboratory experiments under defined flow conditions (Butman et al. 1988; Pawlik et al. 1991).

Invertebrate larvae are exposed to a multitude of environmental factors during their lives in the plankton and at the time of settlement, and undoubtedly they respond to many stimuli in the course of substratum selection. Larvae are known to respond to physical factors, including light, gravity, hydrostatic pressure, salinity, temperature, and water flow (Thorson 1964; Crisp 1984; Sulkin 1984; Young and Chia 1987; Pawlik et al. 1991), and substratum-associated factors such as contour, texture, thermal capacity, and sediment characteristics (Ryland 1974; Raimondi 1988a; Walters and Wethey 1991). But the biological and chemical nature of the substratum has proved to have the greatest influence on larval settlement in both laboratory and field studies (R. R. Strathmann and Branscomb 1979; Mihm et al. 1981; LeTourneux and Bourget 1988; Raimondi 1988b).

The ample literature on the biology of marine invertebrate larvae is filled with anecdotal and experimental accounts of settlement induced by specific substrata; most of these accounts emphasize the importance of chemical signals in mediating larval behavior (reviews in Meadows and Campbell 1972; Chia and Rice 1978; Crisp 1984; Butman 1987; Chia 1989). In this chapter I review the various categories of substratum-specific settlement exhibited by marine invertebrates and then focus attention on studies that have advanced beyond the implication of a settlement cue to the full or partial characterization of a chemical inducer. I do not discuss endogenous chemical signals (hormones) that presumably control the intricate metamorphic processes of most marine invertebrates, about which little is known, nor do I address the inhibition of settlement (antifouling) by chemical means, a topic covered elsewhere (Pawlik 1992; Paul, this volume).



## Site-Specific Settlement

### Aggregative Settlement

The formation of monospecific colonies and aggregations is very common among marine invertebrates. Colonies made up of individuals that are genetically similar or the same (clones) are formed by the asexual division of an initial settler (as in the growth of a coral head from a single polyp) or by the settlement of direct-developing or short-term pelagic larvae near their mother (as with some sponges, ascidians, and bryozoans). The mobile adults of some species aggregate temporarily for the purpose of breeding (Pennington 1985). For most species, aggregations of genetically unrelated individuals are formed by the settlement of planktonic larvae on or near adult conspecifics. This last condition is particularly prevalent among hard-bottom, sessile intertidal organisms, including barnacles (e.g., Knight-Jones 1953; Raimondi 1991), bivalves (Bayne 1969; McGrath et al. 1988), and polychaetes (Wilson 1968; Scheltema et al. 1981). Gregarious settlement has been reported in at least 35 invertebrate species representing eight phyla; in 18 of these there was evidence of a chemical inducer of settlement (Burke 1986).

Gregariousness has many advantages (Crisp 1979; Pawlik and Faulkner 1988). Larvae that settle on or near adult conspecifics have chosen a habitat more likely to support postlarval growth than one chosen indiscriminately. Juveniles may derive additional benefits from the presence of adult conspecifics; for example, juvenile sand dollars that recruit to beds of adults encounter less predation from tanaid crustaceans, which are displaced by the sediment-reworking activities of the adult sand dollars (Highsmith 1982). Adult invertebrates also derive reproductive benefits from aggregation. Proximity increases fertilization success for both internally fertilizing and freely spawning species (Crisp 1979; Pennington 1985). Moreover, individuals in aggregations may live longer than solitary individuals (Wilson 1974) and thereby benefit from greater fecundity over the course of a longer adult life span.

### Associative Settlement

The term *associative settlement* was first used by Crisp (1974) to describe the enhanced or specific settlement of one species on another. Inasmuch as associative settlement results in heterospecific organisms living in close proximity, it can be subdivided into several categories on the basis of the nutritional relationship of the adult or-

ganisms. Nonparasitic associations, or symbioses, between organisms are variously defined as mutualistic (reciprocally advantageous), commensalistic (one party benefits, the other is neither helped nor harmed), inquilinistic (association for protection), epibiotic (association for substratum), and phoretic (association for transport) (Zann 1980). Many invertebrates involved in these symbioses settle as larvae onto their hosts. In most cases, chemical cues are thought to be responsible for this specificity.

Mutualism and commensalism are common in marine communities, particularly in the tropics. Among crustaceans, a variety of shrimps and crabs (representative genera include *Periclimenes*, *Pontonia*, *Pinnotheres*, *Petrolisthes*, and *Trapezia*) are associated with specific host cnidarians, echinoderms, and molluscs (Zann 1980; Stevens 1990). Some barnacles are extremely specialized in their substratum requirements, settling specifically on sponges, gorgonians, hard corals, turtles, sea snakes, or marine mammals (reviewed in Crisp 1974; Lewis 1978; Zann 1980).

Epiphytic associations are common among several species of marine invertebrates that have planktonic larvae. Encrusting red algae promote the settlement of various species of corals (Sebens 1983; D. E. Morse et al. 1988), polychaetes (Gee 1964), and echinoderms (Barker 1977; Rowley 1989), while some bivalves prefer filamentous red algae (Eyster and Pechenik 1987). Brown algae are the preferred substrata of hydroids, spirorbid polychaetes, and bryozoans (Nishihira 1968; Scheltema 1974). Various species of spirorbids settle specifically on red algae of the genera *Corallina* or *Lithothamnion*, sea grasses of the genera *Posidonia*, *Thallasia*, or *Zostera*, or on the shells of crustaceans (Crisp 1974; Dirnberger 1990).

Most invertebrate phyla include parasitic groups; some are made up entirely of parasites. Little is known about how the dispersive stages of marine parasites find their hosts, but it is likely that chemical signals are involved. Molluscan parasites include pyramidellaceans, which are ectoparasites on other molluscs and polychaetes, and coralliophilids, snails that live inside or next to the corals they parasitize (Hadfield 1976).

Among the crustaceans are several parasitic groups with pelagic larval stages, including isopods, copepods, and cirripedes. Perhaps the most specialized of these are the rhizocephalan barnacles, which primarily parasitize other crustaceans (Høeg and Lützen 1985). Female rhizocephalans form dendritic processes in the bodies of their hosts; when mature, each produces a reproductive sac external to the host from which larvae are released. Cyprid larvae are either male or female. The female larva must locate a suitable host to infect, usually a specific crustacean species, while the male larva must settle on the reproductive sac of a virginal female. After injecting spermatogenic cells into the female sac, the male cyprid dies. Considering the unlikelihood of a random encounter between a female cyprid and its host, or, more so, between a male cyprid and a virginal female reproductive sac, the involvement of chemical cues at settlement seems a necessity. In addition, the cyprid larvae of some rhizocephalans lack thoracic appendages and cannot swim (Pawlik 1987), making the chance discovery of a virgin adult female by a male larva even more improbable.



Herbivorous and predatory marine invertebrates with specific food requirements and pelagic larvae are generally thought to settle on or near their prey. Settlement cues are probably involved whenever the prey organisms have highly restricted distributions. Among molluscs, several opisthobranch groups have very narrow food requirements: specific cnidarian prey for most aeolid nudibranchs, sponges for dorid nudibranchs, siphonaceous green algae for ascoglossans, and red algae or cyanophytes for aplysiids (Switzer-Dunlap 1978; Faulkner and Ghiselin 1983; Hadfield and Miller 1987). Some chitons and gastropod molluscs settle specifically on encrusting red algae and feed on the crusts after metamorphosis (Barnes and Gonor 1973; A. N. C. Morse and Morse 1984a).

### Settlement on Microbial Films

The growth of microorganisms on hard substrata or sediments has long been recognized as a prerequisite for the settlement of some invertebrates (Zobell and Allen 1935; Gray 1974; Scheltema 1974). Clean surfaces exposed to seawater go through a succession of changes, beginning with the formation of a primary film of organic material and advancing to the development of a complex microbial community (Mitchell and Kirchman 1984). Although microorganisms promote the settlement of many species, including hydroids (e.g., Müller 1973), polychaetes (Kirchman et al. 1982a), bivalves (Weiner et al. 1985), bryozoans (Mihm et al. 1981), barnacles (LeTourneux and Bourget 1988), and echinoderms (Cameron and Hinegardner 1974), microbial films may inhibit the settlement of others (Maki et al. 1988, 1989).

## The Chemical Nature of Settlement Inducers

Considering the many examples in which marine invertebrate larval settlement has been demonstrated to be highly substratum specific, it is surprising that naturally occurring settlement inducers have

been isolated and identified for only a few species. This lack of knowledge stems largely from the difficulties associated with obtaining competent larvae (i.e., larvae that are developmentally ready to settle). Only rarely can they be harvested directly from the plankton (e.g., Rice 1988); generally, field-caught larvae are difficult to identify and their densities are too low to provide sufficient numbers for replicate experiments. Laboratory culture of larvae is an obvious alternative. It is relatively easy to obtain the gametes of some invertebrates, but other species are notoriously difficult to spawn or maintain narrow reproductive seasons (M. Strathmann 1987). Once sufficient numbers of newly hatched larvae have been procured, they must be maintained in culture for the time necessary for them to become competent to settle. This period is usually short for lecithotrophic (nonfeeding) larvae, but most pelagic larvae are planktotrophic and must be fed for several weeks before competence is attained. Despite the difficulties, experiments have been performed on the responses of several species to chemical cues that have been purified and characterized to various degrees.

### Isolated and Identified Settlement Inducers

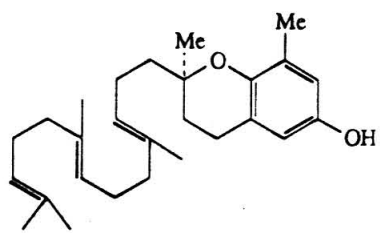
The structures of substratum-derived, naturally occurring compounds that stimulate settlement are known for only four species of marine invertebrates: the hydroid *Coryne uchidai*, the echiuran *Bonellia viridis*, the bivalve *Pecten maximus*, and two subspecies of the polychaete *Phragmatopoma lapidosa*. The information that follows regarding compounds that affect the first three species has been taken primarily from the chemical literature; biological evidence to support their putative function is somewhat equivocal.

*Coryne uchidai* Nishihira (1968) studied the settlement specificity of the hydroid *Coryne uchidai* on brown algae of the family Sargassaceae. When placed in assay dishes containing 20 1-mm$^2$ pieces of *Sargassum thunbergii*, *S. confusum*, or *S. tortile*, larvae of *C. uchidai* stopped swimming immediately and began crawling. In contrast, in dishes without algae or in dishes containing an equal quantity of the green alga *Ulva pertusa*, larvae gradually ceased swimming and began crawling over the course of a day. The abrupt drop to the bottom in the presence of algal exudates resulted from the cessation of larval ciliary activity. Most of the larvae formed polyps within two to three days in dishes containing *S. confusum* or *S. tortile*, within three to four days in dishes containing *S. thunbergii* and *U. pertusa*, and within three to six days in control dishes (no algae).



Boiled aqueous extracts of *Sargassum tortile* similarly caused larvae to cease swimming immediately, with metamorphosis occurring within two days. Extracts of *U. pertusa* had no effect on larvae beyond the gradual settlement observed in control dishes. Extracts of two other algae, *Dictyopteris divaricata* and *Symphyocladia latiuscula* (neither of which belong to the family Sargassaceae), caused immediate cessation of larval swimming but little or no metamorphosis. An extract of the latter alga killed larvae within one day. Choice experiments were performed with extracts incorporated into agar blocks, but the results were ambiguous because the aqueous extracts leached out of the blocks and into the seawater in the assay dishes.

Fractionation of hexane extracts of dried *Sargassum tortile* led to the isolation of several diterpenoid chromanols (Kato et al. 1975). Two of the most abundant chromanols were identified as δ-tocotrienol (1) and its epoxide (2).

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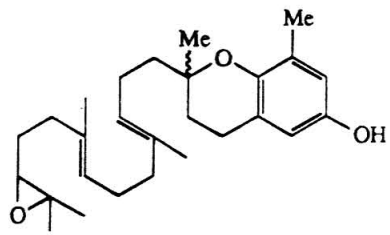


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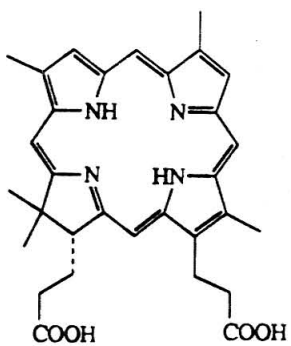
Only limited settlement assay results were provided. Compounds were dissolved in a drop of ethanol and added to 20 ml of seawater containing 10 larvae. After 72 hours, δ-tocotrienol at 37.5 μg/ml seawater induced 3 larvae to metamorphose, but the remaining 7 died after settlement. The epoxide induced all 10 larvae to metamorphose within 72 hours at both 18.8 and 75 μg/ml seawater. None of the larvae in control dishes (ethanol alone) completed metamorphosis within 72 hours.

Unfortunately, no further information is available on the settlement responses of *C. uchidai* to algal metabolites. It is unclear whether chromanols are the only inductive compounds present in *S. tortile*, and whether species of *Sargassum* produce these compounds to the exclusion of nonpreferred algae. Inasmuch as the compounds described are lipophilic, it is unlikely that they are perceived in solution; yet a water-soluble inducer was indicated by experiments with aqueous extracts of algae. It is also unclear whether the chromanols are elaborated by the algae in such a way that larvae would encounter them in nature.

*Bonellia viridis* During the early part of this century, Baltzer (reviewed in Pilger 1978; Jaccarini et al. 1983) discovered that sexually undifferentiated larvae of *Bonellia viridis* were stimulated to settle and metamorphose into nonfeeding dwarf males after contact with the proboscis of an adult female. Larvae that failed to encounter an adult female metamorphosed and developed into females themselves. Male development appeared to result primarily from the inhibitory effects of an unknown factor on female development. Aqueous extracts of the female proboscis and intestine induced metamorphosis into males at concentrations of 1 part dried tissue to 6000–9000 parts seawater. Herbst (in Pilger 1978; Jaccarini et al. 1983) found that similar effects could be triggered by altering the ionic composition or pH of the seawater to which larvae were exposed. Baltzer proposed that the masculinizing factor was bonellin, a green integumentary pigment that had been isolated from adult females in 1875 by Sorby (for a history of chemical investigations of *B. viridis*, see Agius et al. 1979). A century later, the structure of bonellin was described as an uncomplexed, alkylated chlorin (3) (Pelter et al. 1978).

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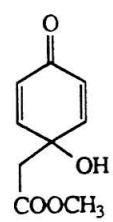
Whereas bonellin was the predominant isolate of the proboscis of *B. viridis*, amino acid conjugates of the compound were present in the body wall of the animal (Cariello et al. 1978; Ballantine et al. 1980). It was suggested that these conjugates of bonellin were stored or scavenged in the body of *B. viridis* and elaborated as bonellin in the proboscis in order to affect larval settlement. Agius (1979), however, found the masculinizing factor in aqueous extracts of proboscides and body tissues, and potent activity in the pigmented body secretion. Larvae were attracted to the proboscides of female worms and absorbed the green pigment from the proboscis at the site of their attachment (Agius et al. 1979). Larval assays performed with purified bonellin resulted in



ambiguous data: at 1 ppm, the compound induced 31.2% of the larvae to differentiate into males, as opposed to 99% in the presence of an adult female and 8.5% in control seawater. Strangely, 0.5 and 0.2 ppm bonellin induced 35.8% and 14.4% masculinization, respectively, but 0.01 ppm bonellin induced 44.5% of the larvae to develop into males.

Results of a more rigorous study were presented by Jaccarini et al. (1983), who concluded that the effects of bonellin on sex determination were inconsistent. Significantly higher levels of masculinization were induced in larvae exposed to $10^{-6}$ M bonellin, but while purified bonellin induced 28% of the larvae to develop into males, the female body secretion triggered 96% masculinization. Moreover, in three of five experiments with purified bonellin, there was no enhanced masculinization over controls. There had been a suggestion that bonellin induced masculinization by a photodynamic effect: the compound is toxic to a wide range of organisms when assayed in the presence of light (Agius et al. 1979; De Nicola Giudici 1984). But comparative larval assays of purified bonellin in light and darkness resulted in no significant effects on controls (Jaccarini et al. 1983). Therefore there is no unequivocal evidence linking bonellin to the masculinizing properties of the body secretion of *B. viridis*. Enhancement of larval settlement on, or attraction of larvae to, the proboscides of female worms has yet to be experimentally assessed.

*Pecten maximus* Yvin et al. (1985) reported that aqueous ethanol extracts of the red alga *Delesseria sanguinea* stimulated settlement of the bivalve scallop *Pecten maximus*. The active component was partitioned into ether, purified by high-performance liquid chromatography (HPLC), and identified as jacaranone (4),

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a compound previously isolated from *Jacaranda caucana*, a terrestrial vascular plant. Jacaranone stimulated maximum settlement of *P. maximus* at 0.5 mg/l ($\sim 3 \times 10^{-6}$ M), with increasing levels of larval mortality at higher concentrations (Cochard et al. 1989). This response does

not appear to be particularly relevant to the biology of *P. maximus*, however, because the species is not known to settle with any degree of specificity on *D. sanguinea*; its recruitment patterns are relatively indiscriminate (Cochard et al. 1989).

*Phragmatopoma* Marine polychaete worms of the family Sabellariidae live in tubes constructed of cemented grains of sand. Some species are gregarious and form colonies and reefs of amassed sand tubes. These colonies are entirely dependent on the recruitment of planktonic larvae for reef maintenance and growth (Pawlik and Faulkner 1988). Wilson (1968, 1974) studied the larval settlement behavior of several sabellariids from British waters, in particular *Sabellaria alveolata*. Settlement was stimulated on contact with adult tubes, tube remnants, or the mucoid tubes of juvenile worms. Factors such as surface contour and roughness, sediment type, water motion, and the presence of surface microorganisms had only a minor influence on larval behavior. The settlement-inducing capacity of the tubes was insoluble in water and unaffected by drying but was destroyed by cold concentrated acid. Wilson concluded that a chemical cue in the tube cement triggered larval settlement in a fashion similar to that proposed for barnacle larvae by Knight-Jones (1953; see Gregarious Settlement, below).

Larvae of *Phragmatopoma californica*, a gregarious sabellariid from the coast of California, also chose the sand tubes of adult conspecifics over other substrata (Jensen and Morse 1984). Sequential extraction of the tube sand of *P. californica* in a series of organic solvents diminished its capacity to induce larval settlement (Pawlik 1986). The inductive activity was retained in the organic extracts of natural tube sand. An active fraction was isolated from the extracts by HPLC, and nuclear magnetic resonance spectrometry and gas chromatographic analysis of the fraction revealed that it consisted of a mixture of free fatty acids (FFAs) ranging from 14 to 22 carbons in length. Extracts of worm-free tube sand from reefs formed by *P. californica* contained concentrations of FFAs sufficient to induce larval settlement (Pawlik 1986).

The FFA fraction isolated from the tube sand of *P. californica* contained predominantly eicosapentaenoic (20:5), palmitic (16:0), and palmitoleic acids (16:1). (In the shorthand notation for FFAs, the number of carbon atoms in the molecule precedes the colon, and the number of double bonds follows.) Of the 9 FFAs that contributed 3% or more to the active fraction, only palmitoleic, linoleic (18:2), arachidonic (20:4), and eicosapentaenoic acids (5–8, respectively) induced larval settlement.



**5** $CH_3(CH_2)_5CH{=}CH(CH_2)_7COOH$

**6** $CH_3(CH_2)_4CH{=}CHCH_2CH{=}CH(CH_2)_7COOH$

**7** $CH_3(CH_2)_4(CH{=}CHCH_2)_3CH{=}CH(CH_2)_3COOH$

**8** $CH_3CH_2(CH{=}CHCH_2)_4CH{=}CH(CH_2)_3COOH$

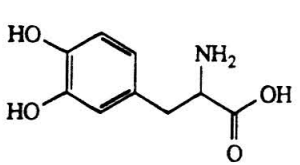
In further assays of an additional 28 FFAs of variable carbon chain length and unsaturation, larval response was stereospecific, with maximum settlement in response to palmitoleic, linolenic (18:3), eicosapentaenoic, and docosahexaenoic (22:6) acids (Pawlik and Faulkner 1986). Palmitelaidic acid, the *trans* isomer of highly active palmitoleic acid, was ineffective at inducing larval settlement. The capacity to stimulate settlement was linked to molecular shape, which is determined both by the number of carbon atoms and the number of *cis* double bonds in the acyl chain. For example, although palmitoleic acid (16:1) was a potent inducer of larval settlement, oleic acid (18:1) was not, as a result of its greater molecular length. Linoleic (18:2) and linolenic acids (18:3) were active, however, because the additional *cis* double bonds act to twist and shorten these molecules to an overall shape similar to that of palmitoleic acid. The induction of larval settlement by FFAs was also dependent on the presence of a free carboxyl group. Modification of the carboxyl terminus of the FFA molecule by esterification or reduction resulted in the loss of inductive activity (Pawlik and Faulkner 1986). Therefore, larval response was dependent on the presence of at least one *cis* double bond in the molecule, conservation of molecular shape with increasing acyl chain length by addition of *cis* double bonds, and the presence of a free carboxyl group. This high degree of stereochemical specificity was likened to that described in studies of chemoreception in terrestrial insects (Pawlik and Faulkner 1986, 1988; see Comparisons with Terrestrial Insects, below).

Larval settlement responses of *Phragmatopoma lapidosa*, a gregarious sabellariid from the tropical western Atlantic, were very similar to those of *P. californica* (Pawlik 1988b). The inductive capacity of the tube sand was lost on extraction and the activity was retained in the extracts. Again, a suite of FFAs was isolated as the active component. The same FFAs that stimulated larval settlement of *P. californica* did so for *P. lapidosa*, and they were isolated from the natural tube sand of both species at about the same concentrations. The similarities did not end there: in addition to having identical larvae and adults, the two species were completely interfertile in reciprocal fertilization experiments. The hybrid larvae of both crosses developed and meta-

morphosed normally, prompting the synonymization of the two species: *Phragmatopoma lapidosa lapidosa* for the western Atlantic subspecies, and *P. l. californica* for the eastern Pacific subspecies.

Larvae of *Sabellaria alveolata*, a reef-building sabellariid from European waters, did not respond to the same chemical signals as responded to by *P. l. californica* (Pawlik 1988a). In reciprocal assays, settlement of both species occurred to a greater extent on conspecific tube sand than on heterospecific tube sand. Extraction of the tube sand of *S. alveolata* diminished its capacity to trigger settlement of conspecific larvae, but the capacity was not transferred to the organic extracts, and an inducer was not isolated or identified. Furthermore, the FFAs that elicited settlement of *P. l. californica* and *P. l. lapidosa* either were not effective at inducing settlement of *S. alveolata* or actually inhibited settlement. Larvae of nongregarious species from the Caribbean, *S. floridensis*, and the eastern Pacific, *S. cementarium*, similarly did not respond to FFAs (Pawlik 1988b; Pawlik and Chia 1991). FFAs were present in the natural tube sand of *S. alveolata* at less than one-tenth the concentration found in natural tube sand of *P. l. californica* and *P. l. lapidosa*, suggesting that adults of the two subspecies of *Phragmatopoma* produce the FFAs that induce conspecific settlement. Pawlik concluded that settlement of different genera of gregarious sabellariids is under the control of different chemical signals. Interspecific differences in larval responses to FFAs further suggested that a specific mechanism is responsible for the perception of FFAs by larvae of the two subspecies of *P. lapidosa*.

Jensen and Morse, who also studied *P. l. californica*, arrived at different conclusions regarding the induction of settlement of this species (Jensen and Morse 1984, 1990; Yool et al. 1986; Jensen et al. 1990). Building on a hypothesis put forth by Wilson (1968), they suggested that some component of quinone-tanned proteins, specifically, an unidentified, cross-linked residue of the amino acid L-β-3,4–dihydroxyphenylalanine (L-DOPA, 9), present in the tube cement of adult worms was responsible for inducing settlement. Larval responses to solutions of L-DOPA were weak at best (Jensen and Morse 1984; Pawlik 1990), but settlement occurred readily in response to the cresol-derived, lipophilic compound 2,6-di-tert-butyl-methylphenol, also known as butylated hydroxytoluene (BHT, 10) (Jensen and Morse 1990).

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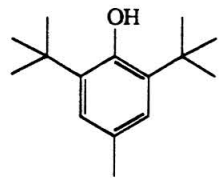


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BHT effected settlement of *P. l. californica* when adsorbed to surfaces in both laboratory and field experiments. Jensen and Morse (1990) proposed that BHT mimics the activity of the unknown, naturally occurring L-DOPA residue from tube cement (but see Pawlik 1990). In addition, the authors questioned whether FFAs function as a natural cue, as proposed by Pawlik (1986; 1988b), suggesting instead that FFAs induce settlement in a nonspecific manner, possibly by operating on the larval nervous system or parallel to the natural inducer (Jensen and Morse 1990; Jensen et al. 1990). In support of their contention: (1) they were unable to detect FFAs on glass beads used by adult worms to make tubes (the natural inducer); (2) freeze-drying and stirring reduced the inductive activity of the natural inducer but not the activity of glass beads coated with FFAs; (3) induction by FFAs was temperature dependent, while induction by the natural inducer was not; and, (4) induction by the natural inducer was taxon specific, but induction by FFAs was not (Jensen et al. 1990).

Do FFAs function as natural settlement cues for larvae of *Phragmatopoma*? Further study is necessary to answer this question. Replication of experiments detailed in Jensen et al. (1990) has failed to confirm that freeze-drying or stirring decreases the inductive activity of the natural inducer as compared with substrata coated with FFAs, or that induction by FFAs is temperature dependent (points 2 and 3 above; Pawlik, unpubl. data). Moreover, the contention that larval response to FFAs is nonspecific (point 4 above) was supported by Jensen et al. (1990) with data from highly variable assays of abalone larvae (*Haliotis rufescens*), while the high degree of specificity of larval response within the Sabellariidae was ignored (Pawlik 1988a, 1988b). But, clearly, if FFAs are absent from inductive, uncontaminated tube sand, the naturally occurring cue must lie elsewhere. Jensen et al. (1990) may be correct in suggesting that the natural tube sand used by Pawlik (1986, 1988b) was contaminated with organic material containing FFAs (possibly oocytes that stuck to sand grains as gravid adult females were removed from their tubes). But if FFAs are not the natural inducers of settlement, then it is unclear why larval responses to these compounds are restricted to the genus *Phragmatopoma* within the

polychaete family Sabellariidae, and why these compounds occur at high concentrations in the natural tube sand of species that respond to them, but not in the tube sand of species that do not (Pawlik 1986, 1988a, 1988b; Pawlik and Chia 1991).

Larval settlement experiments performed in laboratory flumes have several major advantages over those performed in still water; in particular, the ability of larvae to select substrata in flow can be assessed (see Butman 1987; Butman et al. 1988). *P. l. californica* has proven to be a very useful subject in experiments with flumes because (1) the larvae are large enough to be easily seen; (2) they undergo settlement rapidly; (3) metamorphosis results in major morphological changes, permitting the separation of larvae and metamorphosed juveniles in fixed samples; and (4) settlement is highly specific, occurring only on tube sand or sand treated with inductive compounds. Pawlik et al. (1991) conducted flume experiments at two flow regimes in which larvae of *P. l. californica* were offered a choice of five treatment substrata in a five-by-five Latin-square array. In both flows, larvae settled preferentially on the two substrata that had induced settlement in still-water assays (tube sand and sand treated with palmitoleic acid). Surprisingly, delivery of larvae to the array was greater in fast flow, because larvae tended to move off the bottom in slow flow. Therefore behavior may be important in the settlement process at two levels for *P. l. californica*: larvae respond first to flow conditions and then, as they sample the substratum, to chemical cues.

### Partially Purified Inducers

Studies of several invertebrate species described below have proceeded toward characterizing the chemical induction of settlement but have not yet identified the stimulatory compounds. After field observations and laboratory assays indicated preferential settlement of larvae onto a specific substratum, research generally advanced along two lines: (1) various physical and chemical treatments were used in an attempt to destroy the stimulatory capacity, and (2) an effort was made to isolate the inductive factor (often with the use of dialysis tubing) or to transfer it onto an otherwise inactive substratum. If the stimulatory capacity was isolated or transferred, more rigorous chemical separation techniques were often employed.

*Gregarious Settlement* Partially purified inducers of gregarious settlement have been described for several species. Because of their commercial importance, oyster larvae have been the subjects of considerable interest. Crisp (1967) discovered that chemical removal of the organic outer layers of the shell of *Crassostrea virginica* reduced the settlement of conspecific larvae on that substratum, while aqueous extracts of adult animals enhanced settlement. High levels of settlement occurred on tiles treated with lyophilized aqueous extracts of whole oysters or material from aqueous extracts of whole oysters that had been partitioned into diethyl ether (Keck et al. 1971). Hidu (1969) found that settlement of *C. virginica* was stimulated by the water held between the valves of living adults. Larval settlement was promoted by a protein-containing fraction purified from this water (Veitch and Hidu 1971). The protein component had a molecular mass greater than 10 kilodaltons and contained iodinated amino acids. A protease-labile fraction isolated from an oyster tissue extract also enhanced the settlement of *Ostrea edulis* (Bayne 1969). Acetazolamide, an inhibitor of the enzyme carbonic anhydrase, promoted settlement of the New Zealand oyster *Ostrea lutaria*, but its mechanism of action remains unexplained (Nielsen 1973). More recent work on *Crassostrea gigas* has yielded settlement inducers of bacterial origin (Coon et al. 1988; Fitt et al. 1990; see Microbial Films, and Inorganic Compounds as Inducers, below).

Laboratory and field experiments have demonstrated that the sessile gastropod molluscs *Crepidula fornicata* and *C. plana* preferentially settle near adult congeners (McGee and Targett 1989). Larvae of *C. fornicata* exhibited the highest levels of metamorphosis in response to water conditioned by adult conspecifics, but *C. plana* settled in response to water conditioned by either species or by the hermit crab *Pagurus pollicaris*, which inhabits mollusc shells that are often encrusted with adult *Crepidula*. Metamorphosis-inducing activity in seawater conditioned by adult *C. plana* passed through both 10- and 5-kilodalton membrane filters and was retained on a reverse-phase chromatography column (McGee and Targett 1989).

Chemical substances that promote gregarious settlement have been partially purified for the echiuran *Urechis caupo*, the sipunculan *Golfingia misakiana*, and the sand dollars *Dendraster excentricus* and *Echinarachnius parma*. Larvae of *U. caupo* settled rapidly in response to sediments from adult burrows or sediments that had been exposed to the epidermis of an adult worm (Suer and Phillips 1983). The worm-derived factor triggered settlement only when adsorbed onto sediment. It was soluble in seawater and passed through dialysis membrane (3.5–14 kilodaltons), and it was heat labile (>80°C) but stable at ambient seawater temperatures for several days.

Larvae of *Golfingia misakiana* settled in response to a low-molecular-mass (<500 daltons), heat-labile factor present in seawater condi-

tioned by the presence of adult worms (Rice 1988). Larvae of *G. misakiana* did not respond to water conditioned by adults of two other species of sipunculans. In addition to the water-soluble adult factor, sediment covered by a microbial film was required for larvae to begin metamorphosis.

Among echinoderms, chemical induction of larval settlement has been demonstrated most clearly for two species of sand dollars. Highsmith (1982) determined that larvae of *Dendraster excentricus* preferentially settled and metamorphosed on sand from beds of adult conspecifics. The responses of larvae to sand in dialysis tubing and to sand treated with proteolytic enzymes suggested that a small peptide (<10 kilodaltons) was involved. These results were confirmed by Burke (1984), who isolated fractions (by gel-permeation chromatography and HPLC) from extracts of sand from beds of *D. excentricus* that triggered settlement at $10^{-6}$–$10^{-5}$ M. Again, a peptide was indicated as the active component, based on a positive reaction using the Lowry method for protein determination and loss of activity on treatment with proteases. Pearce and Scheibling (1990) demonstrated a similar larval response to conspecifics for the sand dollar *Echinarachnius parma*. Sand could be conditioned by the presence of adults (and thereby rendered capable of inducing high levels of metamorphosis) in the dark and after treatment with antibiotics, suggesting that the cue was derived from conspecifics rather than microflora. The water-soluble inductive factor was destroyed by heating and diffused through dialysis tubing with a pore size of 1 kilodalton.

Svane et al. (1987; Havenhand and Svane 1989) studied the effects of aqueous extracts of adult tissues on larvae of the ascidians *Ascidia mentula* and *Ascidiella scabra* and suggested that larval responses to chemical cues in the adult ascidian tunic may lead to gregarious settlement. *Ascidia mentula* showed aggregated recruitment in the field. Larvae of *Ascidia mentula* placed in the middle of a seawater-filled tube that was sealed at one end with the tunic of a living conspecific adult were preferentially distributed near the tunic after 10 minutes. Embryos of both species were treated with extracts during late development and through hatching, and the percentage of tadpole larvae that had resorbed their tails was scored (metamorphosis irrespective of attachment to the substratum). Conspecific adult extracts enhanced metamorphosis of larvae of *Ascidia mentula* but stimulated metamorphosis of *Ascidiella scabra* before they had hatched. Greater inductive activity was associated with the tunic than with the internal tissues of the adult ascidians. Because the extracts did not trigger other components of normal larval settlement (activation of anterior



papillae), however, it is unclear how the extracted factors function under natural circumstances.

Investigations of the chemical basis for the gregarious settlement of barnacle larvae have a long history, and the topic has been thoroughly reviewed elsewhere (Crisp 1984; Gabbott and Larman 1987). Most barnacle species liberate feeding nauplius larvae that molt through successive stages. In the last larval molt, each nauplius is transformed into a nonfeeding cyprid larva whose sole purpose is to find a suitable site for settlement. Knight-Jones first described gregarious settlement by *Elminius modestus*, *Semibalanus balanoides* (= *Balanus balanoides*), and *Balanus crenatus* (Knight-Jones and Stevenson 1950; Knight-Jones 1953), although subsequent work focused primarily on *S. balanoides* (Crisp and Meadows 1963; Larman et al. 1982). The chemical factor responsible for settlement was highly refractory to physical and chemical treatment, was perceived by cyprid larvae only on contact with factor-treated surfaces, and was present in extracts of several barnacle species, other invertebrates, and a fish (Knight-Jones 1953; Crisp and Meadows 1963; Larman and Gabbott 1975). The factor was identified as arthropodin, a proteinaceous component of arthropod cuticles (Crisp and Meadows 1963).

The settlement-inducing substance was further purified and characterized by Larman and Gabbott (1975; Larman et al. 1982; Larman 1984; Gabbott and Larman 1987). Protein precipitates of boiled extracts of adult *S. balanoides* were separated by electrophoresis to yield two fractions, both containing protein and carbohydrate (>50 kilodaltons), that induced barnacle settlement. Molecules exhibiting similar electrophoretic properties, and similar effectiveness at inducing settlement, were isolated from extracts of other invertebrates and a fish. Exhaustive analyses of boiled and unboiled extracts of *S. balanoides* led to the conclusion that the settlement factor was one (or many) of several closely related acidic proteins, homologous with those described from studies of the cuticles of insects and crustaceans (arthropodins) and with amino acid compositions similar to that of actin. Proteins of this class are sticky; in particular, they adhere well to other proteins. More force is required to remove reversibly attached cyprid larvae (as opposed to those that have begun metamorphosis and cemented themselves for permanent attachment) from extract-treated surfaces than from untreated surfaces or surfaces treated with other proteins (Yule and Crisp 1983; Yule and Walker 1984). Moreover, reversibly attached cyprids left behind proteinaceous "footprints" of their own making, which then might stimulate other cyprids to settle (Yule and Walker 1987). Crisp and Meadows (1963) proposed a mechanism by which cy-

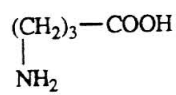
prid larvae detect the settlement factor that relied solely on the stickiness of the inductive proteins (Crisp 1984; Gabbott and Larman 1987). In this instance, settlement was theorized to result from a physical property of the chemical cue (adhesion) rather than from receptor-mediated larval perception, an idea supported by the observed settlement of barnacles on slicks of oil and organometallic compounds (see below). Surprisingly, Crisp (1990) recently found that cyprids of *Balanus amphitrite* settle more readily on conspecific arthropodin than on arthropodins of four other barnacle species, with correspondingly less settlement occurring on the more distantly related species. This is not the expected result if the effects of arthropodins are purely physical. Bourget and colleagues intensively studied the settlement of *S. balanoides* on the Atlantic coast of Canada and concluded that in addition to physical cues, larvae respond to conspecifics (Chabot and Bourget 1988) and to films of microalgae (LeTourneux and Bourget 1988), depending on the spatial scale examined. Mucus has also been observed to affect barnacle settlement (L. E. Johnson and Strathmann 1989). Depending on its source, the mucus either enhanced or inhibited settlement, suggesting that chemical perception rather than stickiness alone may be involved.

*Associative Settlement* Partially purified inducers of associative settlement have been described for species in several phyla. Experimental surfaces treated with extracts of fucoid brown algae elicit the settlement of epibiotic bryozoans, bivalves, and spirorbid polychaetes. Larvae of the bryozoan *Alcyonidium polyoum*, an epibiont on *Fucus serratus*, were induced to settle on surfaces treated with aqueous extracts of the alga (Crisp and Williams 1960). Extracts of two other fucoids, *Fucus vesiculosus* and *Ascophyllum nodosum*, also stimulated settlement. Similar responses were observed for larvae of another bryozoan, *Flustrellidra hispida* (Crisp and Williams 1960). Kiseleva (1966) noted that settlement of the bivalve *Brachyodontes lineatus* was stimulated by aqueous extracts of *Cystoseira barbata*. Extracts of *Fucus serratus* similarly promoted settlement of the epibiotic polychaete *Spirorbis borealis* (Williams 1964). Gee (1964) studied another spirorbid, *S. rupestris*, which settled with a high degree of specificity on the crustose coralline red alga *Lithothamnion polymorphum*. Experimental plates treated with aqueous extracts of *L. polymorphum* stimulated high levels of settlement, and the active factor passed through dialysis tubing with an average pore diameter of 24 Å.

Shipworms are bivalve molluscs that bore into wood. Harington (1921) showed that larvae of the shipworm *Teredo norvegica* aggregated around the dried residue of alcohol or ether extracts of wood, the opening of a capillary tube containing seawater saturated with these extracts, or an aqueous extract of sawdust. Aqueous extracts of wood in the form of bogwater (dissolved humic substances, or *Gelbstoff*) also induced crawling behavior in larvae of the shipworms *Teredo navalis* and *Bankia gouldi* (Culliney 1972).



Larvae of the red abalone *Haliotis rufescens* preferentially settle on crustose red algae of the genera *Lithothamnion*, *Lithophyllum*, and *Hildenbrandia* (D. E. Morse et al. 1980c), although gregarious settlement onto the mucus of adult conspecifics has also been reported for this species (Slattery 1987), and abalone are commercially settled on plates covered with benthic microalgae and bacteria (Hahn 1989). The settlement of *H. rufescens* was first attributed to the presence of γ-aminobutyric acid (GABA, 11)



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molecules "covalently linked" to proteins, and to phycoerythrobilin in the tissues of the algae (D. E. Morse et al. 1979). After further research, however, the settlement factor was limited to a macromolecular fraction isolated from several species of red algae and cyanobacteria but detectable only on the surface of encrusting red algae (A. N. C. Morse and Morse 1984a, 1984b). Treatment of the fraction with proteases or separation by gel-filtration chromatography resulted in the isolation of a group of small (640–1250 daltons), peptide-containing inducer molecules (A. N. C. Morse and Morse 1984a; A. N. C. Morse et al. 1984). The responses of larvae to neuroactive compounds such as GABA are further discussed below and have been reviewed by Hahn (1989) and Pawlik (1990).

Nadeau et al. (1989) reported that larvae of the California sea hare, *Aplysia californica*, did not attain competence to metamorphose when raised in artificial seawater or in natural seawater during the winter months in Woods Hole, Massachusetts. Larvae developed normally when raised in natural seawater during the summer at Woods Hole or during the winter at Hopkins Marine Station, California. This finding suggests that an exogenous factor, absent during the winter in natural seawater off Woods Hole, is required for larval maturation. The factor was inactivated by heating and was retained on 30–100-kilodalton ultrafiltration membranes, but further attempts to isolate it

have been unsuccessful. Nadeau et al. (1989) also found that exudates and extracts of the red macroalgae preferentially eaten by juvenile and adult sea hares promoted larval maturation and subsequent metamorphosis in artificial seawater. They proposed that the source of the factors that induce both competence and metamorphosis is red macroalgae and that the same compound controls both processes. Metamorphosis of *A. californica* can occur on a variety of red, green, and brown intertidal macroalgae (Pawlik 1989), however, so it seems unlikely that the putative factor(s) are restricted to red macroalgae.

Hadfield and colleagues have studied the larval settlement of the nudibranch mollusc *Phestilla sibogae*, an obligate predator of hard corals of the genus *Porites* (Hadfield 1977, 1978, 1984; Hadfield and Scheuer 1985; Hadfield and Pennington 1990). Larvae of *P. sibogae* settled in response to a waterborne inducer released from *Porites compressa* or *Porites lobata*, or in response to seawater containing an aqueous coral extract. The inducer was partially purified and characterized as a small polar molecule (200–500 daltons) with broad temperature and pH stability (0–100°C, pH 1–10). The compound triggered settlement at concentrations as low as a few parts per billion (estimated at $\sim 10^{-10}$ M). Larvae exposed to the inducer prior to becoming competent did not metamorphose once they had fully matured. This habituation was reversed if competent larvae were placed in clean seawater before reexposure to the inducer (Hadfield and Scheuer 1985). Despite intensive efforts, the inducer has not yet been identified (Hadfield and Pennington 1990).

Another nudibranch mollusc, *Eubranchus doriae*, settles preferentially on its hydroid prey, *Kirchenpaueria pinnata* (Bahamondes-Rohas and Dherbomez 1990). Fractions of aqueous extracts of the hydroid, prepared by ultrafiltration, induced metamorphosis of the nudibranch larvae. Various sugars dissolved in seawater ($10^{-4}$ M) also induced metamorphosis, provided that the hydroxyl groups attached to carbons 3 and 4 were in the *cis* position (this category includes galactosamine and hexoses such as D-talose and D-galactose). Affinity chromatography of the inductive fraction indicated the presence of galactosidic residues (Bahamondes-Rohas and Dherbomez 1990).

Preliminary data were gathered on the chemical stimulation of settlement of the barnacle *Membranobalanus orcutti*, an obligate sponge commensal (Pawlik, unpublished data). The barnacle settles on and grows into the surface of two sponges in southern California; only one of these, *Spheciospongia confoederata*, is abundant in shallow waters (Jones 1978). Sponge specimens were collected and freeze-dried, and 2-cm-diameter disks of the sponge surface tissue were punched out



with a cork borer. Fifty cyprids of *M. orcutti* were added to 700 ml of seawater containing a rehydrated sponge disk or the equivalent surface area of living sponge, and the number of metamorphosed juveniles was recorded after 48 hours. Experiments were performed with three replicates. Larvae readily settled on rehydrated sponge disks; 65 ± 2% (mean ± SD) metamorphosed within two days, as compared with 39 ± 13% metamorphosis in response to living sponge. Removal of lipid-soluble constituents of the sponge disks did not have a great effect on settlement: 41 ± 12% metamorphosed on disks that had been sequentially extracted in organic solvents (hexane, diethyl ether, ethyl acetate, and methanol) prior to rehydration. Boiling sponge disks in fresh water for long periods reduced their capacity to stimulate settlement: disks boiled for 5 minutes induced 37 ± 12% metamorphosis, whereas disks boiled for 30 minutes induced only 21 ± 9%. Immersion of sponge disks in a 37% formaldehyde solution for 1 hour (followed by a 24-hour seawater rinse) destroyed their capacity to stimulate settlement; 0.6 ± 1% metamorphosis occurred on these disks, although larvae used in this assay readily settled when subsequently exposed to untreated sponge disks. Similarly, disks treated with 1 mg/ml of a nonspecific protease (fungal pronase, Sigma P5147) for 12 hours in seawater at room temperature (followed by a 24-hour seawater rinse) induced only 5.3 ± 9% metamorphosis. These results suggest that the chemical settlement cue for *M. orcutti* is a relatively refractory protein associated with the surface tissue of the host sponge.

*Microbial Films* Chemical factors produced by microorganisms that elicit the settlement of cnidarians, polychaetes, molluscs, and echinoderms have been partially characterized. Müller (1973) described the settlement of planulae of *Hydractinia echinata*, a hydrozoan, in response to "leakage products" from marine gram-negative bacteria. The active factor was identified as a polar lipid that could be partitioned from a cell-free "leakage solution" into chloroform and was unstable and nondialyzable.

Planulae of the scyphozoan *Cassiopea andromeda* settled in response to a 1–100-kilodalton inducer present in the culture medium of a marine bacterium, *Vibrio* sp. (Neumann 1979). Larvae settled after exposure to various peptides, large proteins, glycoproteins, and cholera toxin, but the relationship of these compounds to the bacterially produced inducer is unknown (Fitt and Hoffmann 1985; Fitt et al. 1987; see Induction by Bioactive Compounds, below).

Larvae of the spirorbid polychaete *Janua brasiliensis* settled preferentially on microbial films cultured from the surface of the green alga

*Ulva lobata* (Kirchman et al. 1982a). Glucose or the lectin concanavalin A (a protein that binds carbohydrate moieties) blocked settlement (Kirchman et al. 1982b). A mechanism of substratum recognition was proposed whereby lectins produced by the larvae bind to specific extracellular bacterial polysaccharides (Maki and Mitchell 1985).

Bonar, Coon, Fitt, Weiner, and their colleagues have produced a body of work on the induction of settlement of oyster larvae (*Crassostrea*) by bacterial products and ammonia. Weiner et al. (1985) isolated a gram-negative, pigment-forming bacterium, designated LST, from oysters and oyster-holding tanks that enhanced the settlement of *Crassostrea virginica*. It was hypothesized that films of LST produce L-dihydroxyphenylalanine (L-DOPA), melanin precursors, and melanin itself, which stimulate larval settlement (Bonar et al. 1985). Coon et al. (1985) discovered that L-DOPA induces settlement behavior of *C. gigas*, thus supporting this hypothesis. Subsequent research revealed, however, that L-DOPA is converted into the neurotransmitter dopamine inside the larva and is not likely to stimulate settlement behavior under natural conditions (Coon and Bonar 1987). A distinction was made between "settlement behavior" (larval foot extension beyond the shell margin) and "metamorphosis" (loss of velum, growth of shell and gill) of *C. gigas*, with separate cues hypothesized for the onset of each (Bonar et al. 1990; Coon et al. 1990a); L-DOPA, for example, induced settlement behavior but not metamorphosis (but see Bonar et al. 1990: table 2). Most recently, the induction of settlement behavior has been attributed to unknown dissolved chemical inducers in the supernatants of cultures of the bacteria *Alteromonas colwelliana* and *Vibrio cholerae* (Fitt et al. 1990). Following size-exclusion chromatography, the inductive activity was retained in a fraction with a molecular mass less than or equal to 300 daltons. Low levels of activity were also detected in the medium used to culture the bacteria (Fitt et al. 1990). Previously, the active component had been identified as dissolved ammonia gas (Coon et al. 1988; Bonar et al. 1990), but this claim has not been repeated (Fitt et al. 1990). Instead, ammonia was proposed as a separate inducer of settlement behavior (Coon et al. 1990b; see Inorganic Compounds as Inducers, below). Metamorphosis of oyster larvae (as opposed to settlement behavior) is thought to be induced by unknown, substratum-associated cues of bacterial origin (Fitt et al. 1990).

Extending the work of Scheltema (1961), Levantine and Bonar (1986) partially isolated a water-soluble factor from sediment that induces metamorphosis of the mud snail *Ilyanassa obsoleta* (= *Nassarius obsoletus*). Ultrafiltration and molecular-sieve chromatography indicated a molecular mass less than 1000 daltons. Analysis of active fractions suggested a high carbohydrate, low protein content.



Cameron and Hinegardner (1974) determined that competent larvae of the sea urchins *Lytechinus pictus* and *Arbacia punctulata* settled in response to a bacterial film or to seawater that had been incubated with particulate material from aquarium filters or sediment from the bottom of seawater storage barrels. The seawater-borne factor was nonvolatile, was removed by adsorption onto charcoal, and had a molecular mass less than 5 kilodaltons.

### Induction by Bioactive Compounds

In contrast to the few systems in which the naturally occurring inducers of settlement have been identified, a profusion of bioactive compounds and neuropharmacological agents are known to have varying effects on mature larvae, ranging from normal settlement and metamorphosis to abnormal metamorphosis and death (reviewed in Pawlik 1990).

Neurotransmitters and their derivatives that affect larval responses include choline and succinylcholine chloride (gastropods: Hadfield 1978; polychaetes: Pawlik 1990), DOPA and the catecholamines dopamine, norepinephrine, and epinephrine (bivalves: Cooper 1982; Coon et al. 1985; gastropods: Pires and Hadfield 1991; polychaetes: Jensen and Morse 1990; Pawlik 1990), and GABA (gastropods: D. E. Morse et al. 1979; echinoderms: Pearce and Scheibling 1990). Bound "neurotransmitter mimetics" have been suggested as inducers of settlement and metamorphosis in a variety of invertebrate larvae (D. E. Morse 1985), but criticisms of this theory have been advanced (Pawlik 1990). In the cases in which naturally occurring settlement cues have been isolated, the compounds are unrelated to neurotransmitters; for example, diterpenes for the cnidarian *Coryne uchidai* (Kato et al. 1975) and free fatty acids for two subspecies of the polychaete *Phragmatopoma lapidosa* (Pawlik 1986, 1988b). Neurotransmitters such as DOPA and GABA are water-soluble amino acids; the capacity of invertebrate larvae to actively transport amino acids into their bodies has been clearly established (e.g., Jaeckle and Manahan 1989). It seems most likely that these neuroactive compounds stimulate larval responses by influencing the larval nervous system internally rather than by acting on an epithelial chemoreceptor (Hirata and Hadfield 1986; Coon et al. 1990a).

Other bioactive substances have been assessed for their effects on invertebrate larvae. Stimulatory compounds include those that alter transmembrane ion transport, such as ouabain (hydroid: Müller 1973) and picrotoxin (gastropods: D. E. Morse et al. 1980b; barnacles: Rittschof et al. 1986), and those that affect the intracellular concentrations of cyclic AMP, such as cholera toxin (scyphozoans: Fitt et al. 1987) and isobutylmethylxanthine (gastropods: Baxter and Morse 1987). The re-

sponses of larvae to these drugs have been used to formulate complex intracellular signal transduction mechanisms controlling metamorphic activation (Baxter and Morse 1987). But behavioral assays of whole larvae have not been specific, either in the application of the drug or in the assessment of the response, and the validity of models of the molecular pathways controlling settlement and metamorphosis has been called into question (Pawlik 1990).

### Inorganic Compounds as Inducers

Some of the earliest research on marine invertebrate larvae concerned the effects of metal salts on settlement and metamorphosis (oysters: Pytherch 1931; Korringa 1940). Copper, iron, and zinc salts have been used to accelerate ascidian and bryozoan settlement (see review in Lynch 1961), although the observed effects have generally been attributed to the toxicity of these compounds.

Elevated concentrations of monovalent cations in seawater induce settlement of many invertebrate species, most probably by affecting the electrical potential across larval cell membranes. Müller and coworkers found that pulsed exposure of larvae of the hydrozoan *Hydractinia echinata* to seawater containing excess $Cs^+$, $Rb^+$, $Li^+$, or $K^+$ induced metamorphosis in a dose-dependent fashion (Spindler and Müller 1972; Müller and Buchal 1973; for earlier work on ionic effects, see Lynch 1961). Ouabain, a cardiac glycoside that blocks active transport of $Na^+$ and $K^+$, inhibited metamorphosis in response to $Cs^+$, $Rb^+$, and $Li^+$, but not to $K^+$, suggesting that the increase in monovalent cations affects the $Na^+$, $K^+$ transport system. Elevated concentrations of $K^+$ have subsequently been found to induce metamorphosis by the molluscs *Haliotis rufescens, Phestilla sibogae, Astrea undosa, Crepidula fornicata*, and *Adalaria proxima* (Baloun and Morse 1984; Yool et al. 1986; Pechenik and Heyman 1987; Todd et al. 1991), and the polychaete *Phragmatopoma lapidosa californica* (Yool et al. 1986). It seems unlikely, however, that invertebrate larvae encounter elevated concentrations of monovalent cations under natural conditions.

Two inorganic gases dissolved in seawater have more recently been reported to stimulate settlement of invertebrate larvae: hydrogen sulfide ($H_2S$) and ammonia ($NH_3$). Cuomo (1985) demonstrated enhanced levels of settlement by larvae of a sediment-dwelling polychaete, *Capitella* sp. I, in the presence of sulfide, with optimal settlement occurring in the 1.0–0.1 mM range. Larvae settled in response to sulfide whether sediment was present or not. Cuomo (1985) suggested that this specific response to sulfide would explain the recruitment of these worms to organically rich sediments. Dubilier (1988) further investigated the settlement of *Capitella* and concluded that the apparent enhancement of settlement in the presence of sulfide was a toxic effect (larvae ceased swimming and lay on the bottom in an apparently anesthetized state), not the response of larvae to a specific settlement cue. She determined that larvae of *Capitella* settled and metamorphosed within minutes in response to organic-rich sediments in the absence of sulfide, whereas addition of sulfide resulted in delayed settlement. Sulfide in the absence of sediment enhanced settlement, but the response required 12–24 hours and resulted in abnormal settlement behavior. Moreover, a similar response was produced by performing the assay in water without $H_2S$, but depleted of oxygen. Larvae of *Capitella* spp. I and II preferentially settled in organically rich sediments in choice experiments performed in a laboratory flume under hydrodynamic conditions similar to those encountered by larvae in nature (Butman et al. 1988; Grassle and Butman 1989); sulfide levels were likely negligible under these experimental conditions.



Geochemical cues such as sulfide might be important settlement stimuli for the pelagic larvae of hydrothermal vent invertebrates in the deep sea (Lutz et al. 1984; VanDover et al. 1988). Vent organisms rely on the oxidation of sulfide as their ultimate energy source, and vent communities are tightly clustered around hydrothermal apertures that discharge sulfide and a wide variety of other inorganic compounds (Coale et al. 1991). The vents are transitory, and the ability to locate new vent sites is of considerable importance for the larvae of organisms adapted to live there.

Ammonia gas ($NH_3$) dissolved in seawater causes larvae of the oyster *Crassostrea gigas* to begin substratum exploration ("settlement behavior" *sensu* Coon et al. 1988; Bonar et al. 1990; Coon et al. 1990a; Fitt et al. 1990); an unknown, bacterially derived, surface-associated cue is required for the subsequent onset of metamorphosis (Fitt et al. 1990). Solutions of $NH_4Cl$ and $(NH_4)_2SO_4$ containing as little as 100 μM $NH_3$ induced larval foot extension, but the response was believed to be the result of increased intracellular pH rather than a specific response to ammonia (Coon et al. 1988, 1990b). Weak bases, such as methylamine and trimethylamine, also induced similar behavior. Ammonia was initially identified as the active agent isolated from bacterial supernatants (Coon et al. 1988; Bonar et al. 1990), a claim that has not been repeated (Fitt et al. 1990). Although ammonia occurs in the water column under natural conditions at concentrations less than an order of magnitude lower than those required for the induction of substratum exploration in oyster larvae, Coon et al. (1990b) suggested that it may play a role in oyster settlement.

Hydrogen peroxide ($H_2O_2$) at $10^{-4}$ M in seawater causes the loss of the velum (swimming organ) in larvae of the nudibranch mollusc *Phestilla sibogae* (Pires and Hadfield 1991). Velar loss occurs as part of the normal process of metamorphosis of gastropod veliger larvae; in this case, the response is probably a toxic one. Invertebrate larval responses to oxidized solutions of L-DOPA and catecholamines are often very different from responses to freshly prepared, unoxidized solutions (e.g., Pawlik 1990), an effect that may be attributable to the production of $H_2O_2$ as these compounds oxidize (Pires and Hadfield 1991).

### Induction by Petroleum Products and Organic Solvents

Holland and co-workers (Holland et al. 1984) discovered that oil extracted from Blackstone oil shale contains a factor that enhances barnacle settlement without deleterious side effects. Settlement of *Semibalanus balanoides* was greater on panels of oil shale than on slate panels in both laboratory and field experiments. Moreover, treatment of shale panels with dichloromethane resulted in even higher levels of settlement, presumably resulting from the mobilization of lipophilic inducers from the kerogen matrix of the shale (Huxley et al. 1984). Smith and Hackney (1989) also found that crude oil or a mixture of gasoline and engine oil spread onto clamshells promoted the settlement of the barnacles *Balanus improvisus* and *B. eburneus*, but petroleum treatment inhibited settlement of the oyster *Crassostrea virginica*.

Hill and Holland (1985) fractionated extracts of oil shale and reported enhanced settlement of *Semibalanus balanoides* and *Elminius modestus* in response to an adsorbed layer of a fraction containing metalloporphyrins. The hydrocarbon and asphaltene fractions inhibited settlement. Thin-layer chromatographic separation of the metalloporphyrin fraction yielded three active bands, two of which were identified by ultraviolet spectrometry as nickel- and vanadium-chelated porphyrins. Settlement was also enhanced by commercially available protoporphyrin IX dimethyl ester when chelated with nickel, vanadium, ferrous, or magnesium ions, but unchelated porphyrin (acid or free base) did not enhance settlement. Maximum enhancement was observed at 0.5–1.0 g metalloporphyrin per square meter, depending on the valence of the chelated metal ion. Metalloporphyrins have been hypothesized to stimulate barnacle settlement in much the same way as arthropodin: the compounds are sticky and presumably bind the proteins associated with the cyprid attachment disk (Hill and Holland 1985; see Gregarious Settlement, above; and Chemosensory Organs, below).



Common organic solvents at high concentrations elicited settlement of the nudibranch *Phestilla sibogae* (Pennington and Hadfield 1989). Five alcohols (including ethanol and methanol), ethanolamine, acetonitrile, acetone, dichloromethane, and toluene were effective at inducing settlement, but ethylene glycol, dimethyl sulfoxide, benzene, and hexane were not. A maximum of 65% settlement occurred in response to ethanol at 0.1 M concentrations after 3–5 days; lethal concentrations of ethanol exceeded 0.75 M.

## Chemoreception and Settlement

In general, naturally occurring chemical inducers of settlement are tactually perceived by marine invertebrate larvae; that is, contact with the substratum is required for recognition of the cue. This has been demonstrated repeatedly and across phylogenetic lines for cnidarians (Donaldson 1974; D. E. Morse et al. 1988), polychaetes (Wilson 1968; Williams 1964; Kirchman et al. 1982a), molluscs (Bayne 1969), barnacles (Knight-Jones 1953), bryozoans (Crisp and Williams 1960), and echinoderms (Highsmith 1982). Settlement can be stimulated by water-soluble neuroactive agents (D. E. Morse et al. 1979; Pawlik 1990) or soluble preparations of inductive substrata (Veitch and Hidu 1971; Müller 1973). Molluscan larvae have been stimulated to settle in enclosed volumes of seawater containing prey species (Thompson 1958) or conspecifics (Hidu 1969) without contacting the respective substrata. Given the turbulent advective processes of waves, tides, and currents, however, soluble compounds are unlikely to be present under natural conditions in sufficient concentrations to influence larvae, except at or very near the surface of the substratum (Crisp 1965; Denny and Shibata 1983). In fact, the few naturally occurring settlement cues that have been isolated and identified are insoluble in seawater (Kato et al. 1975; Yvin et al. 1985; Pawlik 1986).

Nevertheless, soluble compounds are thought to affect settlement in some species. Larvae of the mud snail *Ilyanassa obsoleta* (= *Nassarius obsoletus*) respond to a soluble factor emanating from sediments. In restricted embayments this factor may reach levels that effect cessation of swimming and onset of substratum exploration (Scheltema 1961). Larvae of the coral-eating nudibranch *Phestilla sibogae* may respond to a soluble coral-produced factor as they pass over shallow reefs (Hadfield and Scheuer 1985), although they may not respond until they are very near the substratum (Hadfield and Miller 1987). Similarly, larvae of another nudibranch, *Onchidoris bilamellata*, may begin substratum exploration after perceiving soluble cues associated with their barnacle prey (Chia and Koss 1988).

Marsden (1987) performed laboratory experiments with larvae of the tube worm *Spirobranchus giganteus*, an obligate associate of corals. She noted that in small experimental chambers, precompetent larvae swam toward some coral species in preference to other species, coral rubble, or control seawater, and she suggested that larvae may respond to a chemical cue diffusing from the preferred coral species (Marsden and Meeuwig 1990). In concert with responses to light, this preference would tend to entrain precompetent larvae near the reef, pending their maturation. It has not been demonstrated, however, that the coral diffusate has any effect on larvae at natural concentrations, or that larvae maintain their positions, let alone swim in a directed fashion, under natural conditions of water motion.

Chemotaxis toward a preferred substratum in flowing water has not been documented for the larvae of any marine invertebrate. Crisp (1965) made two persuasive arguments against larval chemotaxis. First, turbulent water flow over a substratum releasing a diffusing inducer would dilute the cue to negligible concentrations within a short distance from the surface. The factor would be present in perceptible quantities only in the viscous boundary layer adjacent to the surface. The depth of the boundary layer under natural flow conditions would be similar to the size of the larva; hence, larval response to a diffusing cue would essentially be contact chemoreception. Second, larvae are small enough to make orientation and navigation in a concentration gradient difficult. Larvae could detect a chemical gradient in one of two ways: (1) by perceiving a concentration difference between sensory organs placed some distance apart—for example, on opposite ends of the larval body; or (2) by integrating concentration changes as the larva moves through the water. The former strategy is unlikely because a concentration difference across the body length of a larva is likely to be imperceptible. The latter is equally implausible because poorly swimming larvae subjected to flow characterized by low Reynolds numbers are more apt to travel along with a mass of water than through it. The sperm of algae (Maier and Müller 1986) and some invertebrates (Miller and King 1983) are attracted to eggs by chemotaxis, but the process occurs over a distance measured in micrometers and within the viscous boundary layer surrounding the egg. Larvae of coral reef fishes appear to respond to diffusable chemical cues emanating from adult conspecifics and heterospecifics (Sweatman 1988), but fish larvae are larger and better swimmers than invertebrate larvae. Juvenile benthic invertebrates apparently respond to soluble cues with directed movements (Rittschof et al. 1983), and chemotaxis certainly occurs among adult marine invertebrates (Atema et al. 1988), which may



obtain directional information from temporal patterns of diffusing chemical signals released into turbulent water flow (Moore and Atema 1988).

### Chemosensory Organs

Sensory organs transduce environmental cues (light, gravity, or mechanical or chemical stimuli) into signals within the organism (neurotransmitters, hormones, or electrical impulses). The sensory organs of invertebrate larvae are poorly known (Laverack 1974; Chia and Rice 1978; Lacalli 1981; Burke 1983; Chia 1989). Their perceptive functions are usually presumptive, inferred from observations of larval behavior or based on histological and ultrastructural evidence. Their small size and delicate nature make larvae poor subjects for neurophysiological investigations. Moreover, because competent larvae are poised for metamorphosis, which usually results in drastic morphological changes, the sensory organs involved in settlement may fulfill their function only at the onset of this crucial transition and may not be subject to repeated experimentation. Considering these difficulties, it is not surprising that no larval chemoreceptive organs that respond to identified chemical signals have been unambiguously characterized, although some recent research shows promise toward this end (Chia and Koss 1988; Arkett et al. 1989).

It is important to note that stimulation of an epithelial sensory organ is not necessarily a requirement for the onset of settlement. There is good evidence that the larval nervous system can be directly influenced to trigger metamorphosis. This has been achieved by exposing larvae to seawater with an altered ionic composition (Baloun and Morse 1984; Yool et al. 1986; see above) and to various neuroactive agents (see above), and by direct electrical stimulation (Cameron and Hinegardner 1974; Satterlie and Cameron 1985). Compounds that "shock" larvae (e.g., $H_2S$) may cause settlement without the involvement of a specific chemoreceptor. There is more evidence, however, that epithelial chemosensory organs play a direct role in larval substratum selection under natural conditions.

The antennules of the cyprid larvae of barnacles were perhaps the first larval structures recognized to have a chemosensory role in selective settlement (Knight-Jones 1953). Cyprid larvae use brushlike disks attached to their antennules to walk over potential substrata at the time of settlement (Nott 1969). Once the settlement site has been chosen, the disks exude a permanent cement and metamorphosis follows. Nott and Foster (1969) described the structure of the attachment disks in some detail. In addition to a complex internal array of muscles,

ducts, and glands, each disk bears a battery of sensory hairs that project beyond its brushlike surface. Three of these sensory hairs have exposed processes and are thought to function as chemoreceptors. Adjacent to the attachment disk, on the fourth segment of the antennule, are additional hairs that may play a chemosensory role (Gibson and Nott 1971). Nott and Foster (1969) proposed a mechanism by which the attachment disks might be employed in detecting the arthropodin cue of conspecific adults: the disks expel proteases as they contact the substratum, resulting in the localized breakdown of arthropodin and the release of characteristic amino acids that are then recognized by the sensory hairs. As I mentioned earlier, an alternative view, the "tactile chemical sense," was elaborated by Crisp and Meadows (1963; Crisp 1974, 1984), who proposed an analogy to an antigen-antibody reaction whereby the attachment disk adheres to the substratum-bound inducer by noncovalent bonding. In this scenario, chemoreception per se would not be involved. This idea has gained support through studies of the temporary attachment of cyprids to variously treated surfaces (Yule and Crisp 1983) and with the discovery of sticky proteins exuded by the attachment disk during reversible attachment (Walker and Yule 1984; Yule and Walker 1987).

The presumptive chemosensory organs of molluscan larvae have been described for a few species. Bonar (1978) characterized the cephalic sensory organ of veliger larvae of the obligate coral-eating nudibranch *Phestilla sibogae*. The organ, located between the lobes of the velum, is made up of three types of cells. Of these, flask-shaped ciliated cells with direct axonal connections to the larval nervous system may have a chemosensory function. Chia and Koss (1982) described the putative sensory organs of the larvae of *Rostanga pulchra*, a nudibranch that settles specifically on its sponge prey, *Ophlitaspongia pennata*. Competent veligers of *R. pulchra* bear two cylindrical rhinophores between their velar lobes. The core of each rhinophore contains a ganglion from which dendritic terminals form tufts at the apex. These dendritic endings were postulated to serve a chemosensory function. The veligers of a third nudibranch, the barnacle predator *Onchidoris bilamellata*, possess two sensory fields on the surface of the larval propodium (the structure used for crawling, which later becomes part of the adult foot; Chia and Koss 1989). Sensory cells of each field are directly innervated by a pair of ganglia located just below the propodial epidermis. The propodial ganglia and their associated sensory structures were hypothesized to detect the chemical factor produced by adult barnacles that stimulates cessation of swimming and onset of substratum exploration (Chia and Koss 1988; Chia 1989). Arkett et al. (1989) have made preliminary intracellular recordings from cells in the sensory field of *O. bilamellata* larvae. These cells respond to barnacle-conditioned seawater with a slow, small-amplitude depolarization but do not respond to control seawater. Injection with lucifer yellow revealed the depolarizing cells to be flask shaped with dendritic processes extending to the propodial surface.



Based on the responses of larvae to various pharmacological and neuroactive agents, Morse and colleagues have proposed a complex dual-pathway system controlling the induction of settlement and metamorphosis of the abalone *Haliotis rufescens* (D. E. Morse 1990; see above). The receptors for both the natural settlement inducer (derived from encrusting red algae) and the waterborne amino acids that regulate this induction may be located on epithelial chemosensory cilia. D. E. Morse et al. (1980a) described the secretion of glycopeptides from the cephalic sensory organ as larvae underwent "behavioral metamorphosis" in response to GABA, a neurotransmitter thought to act at the same receptor as the naturally occurring inducer. After exuding glycopeptides, larvae subsequently shed the ciliated cells of the velum. Trapido-Rosenthal and Morse (1986) determined that a radiolabeled settlement inducer, baclofen (an analogue of GABA), became dissociated from metamorphosing larvae after 20 hours of incubation, evidently coinciding with the loss of velar cells and other epithelial cilia. The authors concluded that chemosensory receptors specific for the induction of settlement were present on these cilia. Purification of mRNA from preparations of cilia followed by cDNA synthesis and amplification revealed mRNA sequences that apparently code for specific proteins involved in transducing the chemosensory signal (Wodicka and Morse 1991). It is not clear, however, whether these cilia are from the velum, the cephalic sensory organ, or elsewhere on the larval surface.

Barlow (1990) noted that GABA effected a cessation of velar ciliary beat in both precompetent and competent larvae of *H. rufescens*. Restrained larvae exposed to GABA exhibited foot movements that were thought to be a component of normal settlement behavior. Using intracellular recording techniques, Barlow monitored electrical responses of velar cells to GABA and determined that the receptor for the compound was most likely not present on velar cells, though her results did not necessarily preclude their presence on velar cilia. She pointed out that the location of putative GABA receptors is unclear: they may be internal (synaptic) or epithelial (chemoreceptive).

Among polychaetes, the larval sensory organs involved in settlement are perhaps best characterized for the reef-building sabellariids

of the genus *Phragmatopoma*. Eckelbarger (1978) described tufts of cilia scattered over the bodies of *Phragmatopoma lapidosa lapidosa* larvae and suggested that these structures may have a role in substratum selection because they are concentrated on parts of the body used when exploring the substratum. Amieva and Reed (1987; Amieva et al. 1987) used video microscopy to study the behavior of *P. l. californica* at settlement and examined the ultrastructure of the larval tentacles of this subspecies. They determined that the tufts of cilia on the tentacle surfaces are immotile and borne by cells in direct communication with the larval nervous system. The morphological evidence and observations of settlement behavior led them to suggest that the ciliary tufts may be involved in the perception of settlement cues.

Ultrastructural studies of marine bryozoan larvae have revealed several structures that may have sensory functions (Reed 1988a; Reed et al. 1988). The putative larval chemosensory organ consists of a long bundle of cilia, called the vibratile plume, which projects from the larva's anterior midline (Reed 1988b). The ciliary bundle is attached to a glandular and sensory complex, the pyriform organ. The cells bearing the vibratile plume appear to be directly innervated. The chemosensory role of the vibratile plume and pyriform organ is corroborated by observations of larval behavior at settlement: bryozoan larvae press their pyriform organs against potential substrata and beat the surface with their vibratile plumes.

Less is known of potential larval chemosensory organs in other invertebrate phyla. Vandermeulen (1974) and Chia and Koss (1979) described putative sensory cells that might mediate substratum selection in the planulae of a coral and an anemone, respectively. Burke (1980) reported sensory cells on the tube feet of the adult rudiment of competent echinoid larvae that may detect cues as the tube feet contact the substratum. Ascidian tadpole larvae bear peripheral ciliated sensory neurons in the anterior adhesive papillae that may detect chemical properties of the substratum (Torrence and Cloney 1988).

### Comparisons with Terrestrial Insects

The chemical ecology of terrestrial insects is much better understood than that of marine invertebrates. Compounds responsible for various insect behaviors have been isolated and identified, the chemosensory structures involved in signal perception have been well characterized through the use of electrophysiological techniques, and the neuroendocrine mechanisms controlling development have been intensively studied (Hansen 1978; Vinnikov 1982; Downer and Laufer 1983; Bell and Cardé 1984; Prestwich 1985; O'Connell 1986).



With regard to larval ecology and substratum selection, there are pronounced differences between insects and benthic marine invertebrates. Among most terrestrial insects the adult is the dispersive phase in the life history, and the larva is sedentary. The diets of adult and larval insects may differ radically, much like their marine counterparts, but the food selected for larval growth is chosen by the egg-laying adult: substratum selection is an adult, rather than a larval, concern (Fig. 6.1). Gregariousness, with all its concomitant advantages, occurs commonly among insects, but for most species it is restricted to adults. Substratum selection, aggregation, and mate location are all mediated by chemical signals in insects, and the cues may be volatile or surface associated, perceived by olfactory or tactile chemoreceptors, respectively. Finally, unlike marine invertebrates, chemical signals involved in the onset of insect metamorphosis are largely endogenous (hormones) rather than exogenous.

Substratum selection by ovipositing adult insects is common. Mobile females are generally stimulated to lay eggs only in response to specific host-produced natural products. For example, pierid butterflies oviposit only on plants of the family Cruciferae that produce glucosinolates (Chew 1977), sawflies lay eggs only on willows that synthesize specific phenolic glycosides (Roininen and Tahvanainen 1989),

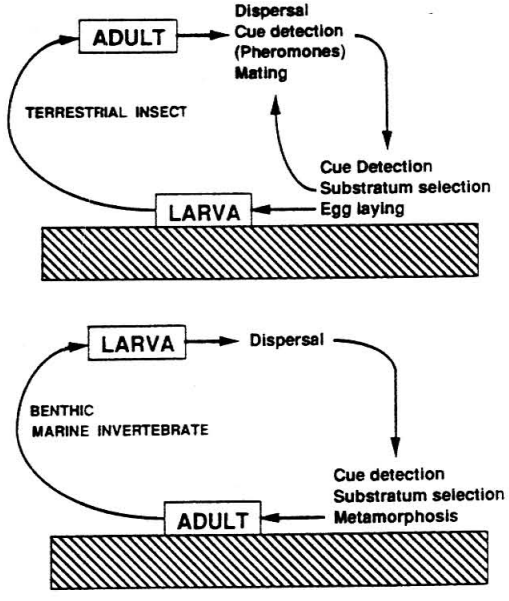


**Figure 6.1** Comparison of the generalized life histories of (a) a terrestrial insect and (b) a benthic marine invertebrate. Terrestrial insect larvae are sedentary, and dispersal and substratum selection are undertaken by the adults; among marine invertebrates, however, it is the larvae that disperse and select the final substrate, where they metamorphose into sendentary adults.

and some parasitic wasps are stimulated to oviposit on caterpillars by specific hydrocarbons produced by the host (Vinson 1984). Larvae of these species are essentially sessile; they are unlikely to find another host if the one chosen by the ovipositing female is unsuitable (Chew 1977). Aggregation pheromones similarly act on adult, rather than larval, insects, and their production is often a response to the presence of food (e.g., beetles: Birgersson et al. 1988; Oehlschlager et al. 1988).

Insect olfactory cues have received particular attention (Kramer 1978; O'Connell 1986). Volatile compounds are used as sex attractants; as trail markers; as alarm, aggregation, or repulsion pheromones; and as indicators of food availability. Chemical communication of this kind may be very complex, requiring suites of several individual compounds in specific ratios. Contact chemoreception is also common among insects, especially in food and mate recognition (Städler 1984; Prestwich 1985). The sensory structures (sensilla) responsible for both olfaction and contact chemoreception have been characterized morphologically and electrophysiologically (Hansen 1978; Städler 1984).

The sensory organs associated with the antennules of barnacle cyprid larvae have been compared to those of other arthropods, including insects (Nott and Foster 1969; Gibson and Nott 1971). Some authors have compared chemically mediated substratum selection of invertebrate larvae to pheromonal communication by terrestrial insects (Burke 1984, 1986; Pawlik and Faulkner 1986, 1988), although insects differ in being able to detect volatile pheromones at great distances from their sources. Gregarious settlement of the polychaetes *Phragmatopoma lapidosa californica* and *P. l. lapidosa* was induced on larval contact with specific free fatty acids isolated from the tubes of adult worms (Pawlik and Faulkner 1986; Pawlik 1988b); among insects, specific fatty acids stimulate electrophysiological responses in sensory receptors of *Necrophorous* beetles (Boeckh 1962) and fleshflies (Shimada 1978).

Metamorphosis is under the control of endogenous chemical signals in both hemi- and holometabolous insects, although environmental cues such as temperature and photoperiod play a role in timing the event. A balance of competing hormones—ecdysone and juvenile hormone—produced by the prothoracic gland and brain, respectively, dictate the advancement of the larva through successive molts, pupation, and to adulthood (Downer and Laufer 1983). In barnacles, synthetic analogues of insect juvenile hormones trigger metamorphosis without attachment (Gomez et al. 1973; Freeman and Costlow 1983), and compounds similar to insect juvenile hormones have been identified in extracts of crustaceans (Laufer et al. 1987). Fouling barnacles



could potentially be controlled by disrupting normal development through the manipulation of the endocrine system (Fingerman 1988), a method already used to control pest insects.

Advances in the study of insect chemical ecology have led to the use of pheromone analogues in pest control (O'Connell 1986). Similar potential may exist for research into the chemical ecology of marine invertebrates. For example, parasitic rhizocephalan barnacles attack commercially important crabs worldwide and prevent them from reproducing or reaching marketable size; their impact on crustacean fisheries can be considerable (Lester 1978; P. T. Johnson et al. 1986). Isolation and identification of the compounds responsible for the localization of host crabs by female cyprids, or virginal externae by male cyprids, could lead to control measures similar to those used to manage some insect pests.

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